19 Decomposition and accumulation of organic matter

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The amount of accumulated organic matter differs markedly between the various IBP tundra sites both in concentration and depth. On the highly mineral alpine and high arctic fellfields, such as the Devon Island beach ridge and plateau, and Maria Pronchitsheva Bay fellfield, significant quantities of dead organic matter occur only in the immediate vicinity of scattered vascular plants. At the opposite extreme are peat sites such as the Moor House, Glenamoy, Stordalen and Signy Island bogs and Macquarie Island herbfields, where highly organic deposits extend to depths of up to several metres (Brown & Veum, 1974; Rosswall & Heal, 1975; Everett, Vassiljevskaya, Brown & Walker, this volume). Over the tundra sites from Devon Island beach ridge to shrub tundra sites in Greenland and South Georgia annual net primary production varies 30–50-fold with comparable variation in the amount of accumulated organic matter (Table 19.1). Differences in soil organic matter reflect differences in many other soil properties and in other parameters of ecosystem function. All climatic zones possess the potential for large accumulation, and different sites within a

Table 19.1. *Estimates of organic matter accumulated in various tundra sites. (Derived from Brown & Veum, 1974)*

Site		Organic matter (kg m^{-2})	Depth (cm)
Signy Island:	*Chorisodontium*	40	15
	Drepanocladus (wet)	35	23
	Grassland	42	15
Devon Island:	Beach ridge	9	62
	Mesic meadow	51	31
Point Barrow:	Grass–sedge meadow	37	20
Hardangervidda:	Lichen heath	8	18
	Dry meadow	30	45
	Wet meadow	45	30
	Birch wood	33	45
Abisko:	Stordalen mire	100	100
Moor House:	Blanket bog	100	100
	Juncus peaty gley	33	30
	Limestone grassland	19	15
Glenamoy:	Bog	400	400

climatic zone often show wide variation, e.g. the Devon Island sedge meadow, beach ridge, and plateau.

Where conditions for primary production are favourable, tundra sites tend to have larger pools of dead organic matter, particularly in relation to primary productivity, than do tropical and subtropical systems. This observation indicates that decomposition processes are inhibited, by the low temperature, short active season and other characteristics of high latitude, to a greater degree than is primary production, resulting in past or current accumulation of organic matter. The accumulation of energy and essential nutrients in dead organic matter subsequently inhibits the rate of mineral nutrient cycling. Tropical systems maintain their high productivity, in part, by a very high rate of decomposition and nutrient turnover.

Accumulation of organic matter results from a past or present imbalance of energy input through net primary production and energy loss through heterotrophic respiration. The activities of herbivores and carnivores, while they may have important effects upon plant populations and processes, never account for a large proportion of the energy flux out of the ecosystem. In this paper, decomposition is taken to be the sum of physical, chemical and biological processes occurring in dead organic matter (including standing dead plant remains, surface and root litter and organic matter in the soil), which results in the reduction of particle size and the transformation of organic carbon compounds to smaller molecules and, ultimately, to gaseous carbon and water, with concomitant liberation of heat energy. The transformation of mineral elements from organic to inorganic form, allowing their recirculation through the ecosystem (Goksøyr, 1975), is part of the decomposition process.

Decomposition, as broadly defined here, embraces many processes involving different organisms, reactants and end-products. In some cases these processes are performed 'in parallel' by different organisms acting upon and competing for the same substrate; in other cases the processes are linked serially, one organism acting upon a substrate formed as an end-product of the activity of another organism. In all cases, organisms are selected, not for their contribution to the overall rate of decomposition, but for their ability to maximise their own rates of growth and reproduction. Obviously an organism's contribution to decomposition is related to its growth and reproduction, but not always in a simple way.

There are two basic approaches to the study of decomposition (MacLean, 1974). One approach focuses upon the organisms responsible for decomposition, while the other focuses upon the substrate available for decomposition and its changes in quantity and quality over time. Since microorganisms are primarily responsible for decomposition, the first approach is largely the domain of microbiology (Holding, this volume). In the present paper we emphasise studies which use techniques such as litter weight loss,

cellulose weight or tensile strength loss, rates of oxygen uptake and carbon dioxide evolution *in situ* and in the laboratory – techniques that integrate the activities of the complex of organisms active upon the particular substrate studied. Our intent is to interpret the patterns of organic matter decomposition, and its inverse, accumulation, in the variety of sites comprising the IBP Tundra Biome, with respect to the biotic and abiotic factors which prevail at those sites. This chapter is based mainly on the detailed information published in Holding, Heal, MacLean & Flanagan (1974), Rosswall & Heal (1975) and Wielgolaski (1975*a*, *b*). The concepts of decomposition developed here are formalised in the simulation models described by Bunnell & Dowding (1974), Bunnell & Tait (1974), Bunnell & Scoullar (1975), and Bunnell & Scoullar (this volume).

The environmental setting

Abiotic variables

The seasonal air temperature pattern suggests that the IBP sites are distributed over gradients of latitude, which primarily affects the length of the decomposition season, and continentality, which affects the summer and winter temperatures (Fig. 19.1). All of the polar sites plus Stordalen and
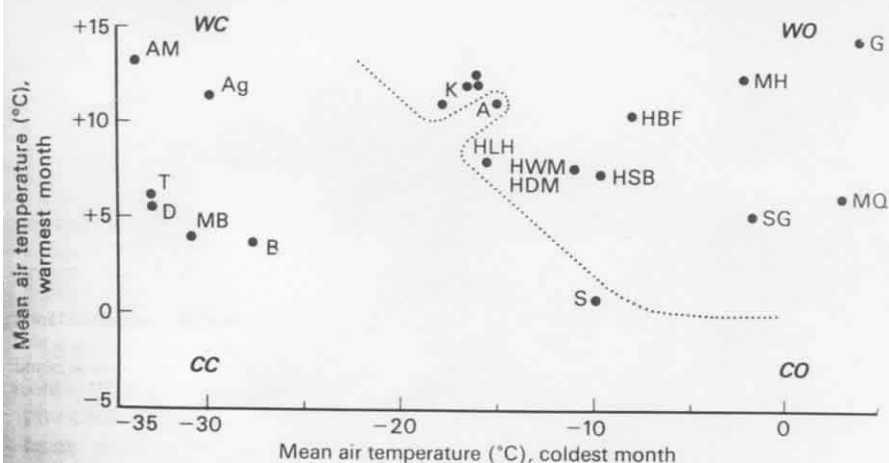

Fig. 19.1. The distribution of IBP tundra sites in relation to temperature. The permafrost line (.....) and the general position of cold continental (*CC*), cold oceanic (*CO*), warm continental (*WC*) and warm oceanic (*WO*) regimes are shown. Site initials are AM – Ary-Mas, Ag – Agapa, T – Tareya, D – Devon Island, MB – Maria Pronchitsheva Bay, B – Point Barrow, K – Kevo (4 sites), HLH – Hardangervidda lichen heath, HWM – Hardangervidda wet meadow, HDM – Hardangervidda dry meadow, HSB – Hardangervidda snowbed, HBF – Hardangervidda birch forest, A – Abisko Stordalen, S – Signy Island, SG – South Georgia, MQ – Macquarie Island, MH – Moor House, G – Glenamoy.
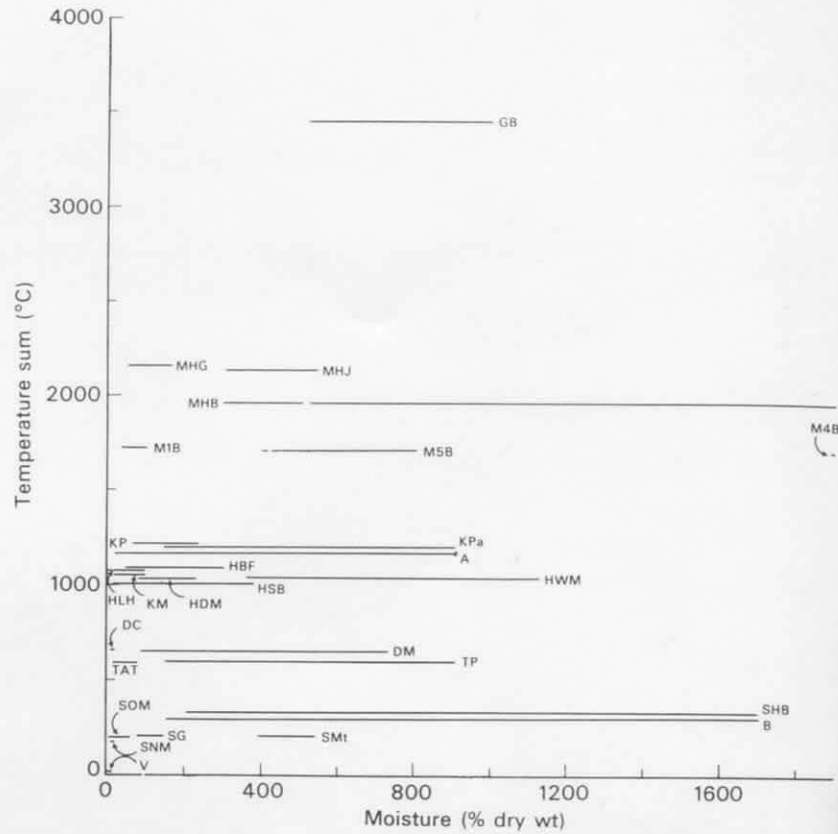
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Fig. 19.2. The range of moisture conditions, expressed as percentage of dry weight, in the surface layers of some Tundra Biome sites, related to the temperature regime, expressed as the sum of day degrees above 0 °C. Data from French (1974). Site initials are B – Point Barrow, V – South Victoria Land, SNM – Signy Island new moraine, SOM – Signy Island old moraine, SMt – Signy Island mountain, SHB – Signy Island Hut Bank, SG – South Georgia, TAT – Tareya *Astragalus–Dryas* tundra, TP – Tareya polygon centre, DC – Devon Island beach ridge crest, DM – Devon Island meadow, HLH – Hardangervidda lichen heath, HDM – Hardangervidda dry meadow, HSB – Hardangervidda snowbed, HWM – Hardangervidda wet meadow, HBF – Hardangervidda birch forest, KM – Kevo mountain heath, KP – Kevo pine (and birch), KPa – Kevo palsa, A – Abisko Stordalen, M1B, M4B and M5B – Macquarie Island subsites, MHB – Moor House blanket bog, MHG – Moor House grassland, MHJ – Moor House *Juncus*, GB – Glenamoy bog.

Signy Island have permafrost, the Stordalen mire being in the Abisko area where permafrost occurs only under particular soil conditions.

The most important climatic parameters for decomposition are: (1) the length and temperature of the active season; and (2) the supply and seasonal availability of moisture. The length and temperature of the active season are integrated by the measure cumulative degree days above a threshold. In this case 0 °C provides a useful threshold, although some decomposition pro-

cesses may continue at temperatures below 0 °C. The difficulties associated with such a linear integration of temperature (Remmert & Wunderling, 1970; Solhøy & Skartveit, 1975) are not likely to be of great importance at the level of resolution sought here.

Moisture conditions in the litter and soil reflect both the precipitation–evaporation balance at the site and local soil drainage conditions. There is no broad pattern of soil moisture along latitudinal or temperature gradients (Fig. 19.2). Very wet soils (>1000 % dry wt moisture) occur throughout the range of sites, often adjacent to dry soils (e.g. Devon Island, Hardangervidda). At the more continental sites, low precipitation and relatively high temperatures in summer may result in drying conditions and a wide annual variation in the moisture content of the soil and particularly the surface litter and standing dead plant remains. At the more oceanic sites, even with high summer temperatures, there is usually a moisture surplus. The Glenamoy site represents an extreme combination of warmth and wetness. In the wet meadow and bog sites anaerobic conditions tend to develop, particularly during summer.

Although the general temperature and moisture characteristics of the sites can be readily described it is important to recognise the large variation in conditions which can occur over small distances, both horizontally and within the soil profile. The presence of permafrost exaggerates the effect of local differences in topography upon drainage and site moisture conditions, so that habitats separated by a few centimetres in height may differ markedly in soil moisture. The diurnal variation in temperature, especially in the surface layers, is widely recognised; large diurnal fluctuations in moisture content may also occur. Small variations in vegetation cover, in aspect or topography, can have a large effect on the microclimate of decomposing material. Such differences in microhabitats can be as large as those between sites that are geographically widely separated.

A wide range of soil types occurs across the tundra sites. Lithosols and regosols, poor in organic matter, occur in alpine and polar areas where frost action is severe and glaciation recent. Podzols and peats are widespread, but brown earths are confined to a few sites (Signy Island, Moor House). There is no obvious pattern over the biome. These soil types show wide variations in pH and in available nutrients (pH, 3.5–7.5; nitrogen, 0.1–2.6 %; phosphorus, 1–500 (−1500) ppm; potassium, 10–600; calcium, 5–10 000) again without a marked pattern between sites (Brown & Veum, 1974; French, 1974; Everett *et al.*, this volume).

Substrates for decomposition

Input from primary production to the decomposition cycle varies in both quantity and quality. Net primary production varies from less than 25 g m^{-2} year^{-1} on the beach ridge crest and plateau habitats at Devon Island,

where plant cover is discontinuous, to more than 1000 g m^{-2} year^{-1} in the most productive shrub tundras of Niwot Ridge, South Georgia, Greenland and Macquarie Island.

The life-form of the vegetation gives rise to differences in chemical composition of the litter (Table 19.2). Herbfields, meadows and mires dominated by monocotyledons produce remains that are low in lignin (<25 %) and have moderate concentrations of soluble constituents (<25 %) and mineral nutrients (C:N 30–50). On the heaths, bogs and fellfields the production contains a much higher proportion of woody tissue, with lignin concentrations of 25–40 %, a low soluble fraction (<10 %), and low nutrient concentration (C:N 60–120). Mosses, which are a major component of bog vegetation, also have low nutrient concentrations, and concentrations of plant compounds that may inhibit consumption by animals and attack by decomposer micro-organisms. On the drier heaths and fellfields lichens contribute significant amounts of material for decomposition which are low in lignin and cellulose, but high in hemicellulose, and thus may require different decomposer organisms. The perennial habit of most of the vegetation and the conservation of nutrients and soluble organic compounds by translocation at the end of the growing season further decreases the content of nutrients and readily decomposable materials in tundra litter compared with other biomes.

Some variation in physical and chemical composition of input results from herbivore activity. Grazing ungulates and rodents select vegetation which is low in lignin, digesting most of the easily soluble compounds to produce faeces with high cellulose content, but also high nitrogen content and moisture-holding capacity compared with plant litter. Winter grazing by lemmings and muskox, in particular, also converts standing dead vegetation to litter, where it experiences a different temperature and moisture environment for decomposition. This phenomenon is especially obvious at melt-off in years when lemming populations are high (Batzli *et al.*, this volume).

Decomposer populations

Physical and chemical processes such as leaching and physical breakdown of substrates due to freeze–thaw cycles are an important part of the decomposition process. However, decomposition rates and their variation between sites are largely determined by the abundance and rates of activity of decomposer organisms. Details of the microflora at IBP tundra sites are given by Holding (this volume).

Micro-organisms associated with decaying organic matter in tundra belong to taxonomic groups which are common in other biomes, but the number of taxa and the biomass are generally lower than in other biomes.

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Table 19.2. *Chemical composition of some litters from tundra sites, expressed as a percentage of dry weight. From Flanagan & Veum (1974), Bunnell (1973), Wielgolaski, Kjelvik & Kallio (1975), Heal et al. (1978)*

	Ash	N	P	K	Ca	Mg	Ethanol soluble	Soluble carbohydrate	Cellulose	Lignin
Point Barrow										
Carex aquatilis (l)	5.2	—	—	—	—	—	11.7	—	43.8	27.7
Eriophorum angustifolium (l)	4.2	1.3	0.1	0.2	0.4	—	6.8	—	43.4	33.0
Total litter	4.8	1.1	0.1	0.2	0.3	—	5.4	—	38.7	39.9
Hardangervidda										
Lichen heath (m)	11.8	1.0	0.06	0.1	0.2	0.04	—	—		
Dry meadow (m)	7.9	1.5	0.10	0.2	1.7	0.07	—	—		
Wet meadow (m)	7.5	1.8	0.11	0.1	1.0	0.04	—	—		
Birch forest (m)	5.6	1.1	0.08	0.1	0.5	0.10	—	—		
Moor House	.									
Rubus chamaemorus (l)	—	1.3	0.07	0.09	0.85	0.53	—	8.2	34	6
Eriophorum angustifolium (l)	—	0.9	0.05	0.11	0.71	0.12	—	5.7	57	23
Calluna vulgaris (sh)	—	1.4	0.07	0.09	0.34	0.06	—	4.2	42	39
Calluna vulgaris (st)	—	0.6	0.04	0.03	0.11	0.02	—	1.3	68	31
Eriophorum vaginatum (r)	—	0.5	0.06	0.21	0.11	0.08	—	4.5	65	34

l – leaves; sh – shoots; st – stems; r – roots; m – mean for vegetation at site.

Of the soil microflora commonly occurring in other biomes the following were rare or absent in the IBP tundra sites: autotrophic, iron, cellulolytic, nitrogen-fixing and nitrifying bacteria, actinomycetes and the fungal genera *Trichoderma*, *Aspergillus*, *Fusarium* and *Botrytis*. Basidiomycetes were uncommon in many sites but many of the sterile mycelial forms so common in tundra sites may be basidiomycetes. Tests of the biochemical capabilities of isolates from tundra sites indicate that there were no features which distinguish them from microbial populations in other areas (Flanagan & Scarborough, 1974; Rosswall & Clarholm, 1974). Thus, although the range of taxa in tundra may be restricted, those groups which are present appear capable of performing the major processes of organic matter decomposition. It is possible, however, that the limited range of taxa may retard the breakdown of complex molecules which require for their catabolism a succession of organisms or groups of organisms with enzyme versatility.

The extent to which the decomposition potential of the microflora is realised depends largely on environmental conditions. The rate of processes is obviously limited by temperature in tundra, but adaptation, and selection of psychrophilic and cold-tolerant forms, have resulted in microbial populations of which a considerable proportion has a temperature optimum below 20 °C and many of the bacteria and fungi are capable of growth and substrate utilisation around 0 °C. Although the temperature range may be limited for any one species, the range of optima varies between species and, at least for some processes, a sequence of organisms is capable of maintaining the rate of a process over a wide temperature range (Flanagan & Scarborough, 1974).

Anaerobic and acid conditions occur widely in tundra sites through waterlogging with the result that anaerobic bacteria, including methane-producing and sulphate-reducing forms, are common. Both facultative and obligate anaerobic bacteria occur, allowing activity over a wide and fluctuating range of conditions, but the acid conditions tend to favour fungal rather than bacterial populations and activity.

Tundra sites show a clear pattern of reduction in diversity of invertebrate species with increasing latitude, reflecting both biogeographic isolation and climatic severity (Ryan, this volume). Faunal diversity and composition at alpine or 'edaphic' (e.g. Stordalen mire) tundra sites may be strongly influenced by the proximity of adjacent species-rich areas (MacLean, 1975). The reduction in diversity does not occur equally in all taxonomic and functional groups (MacLean, 1975; Ryan, this volume). With increasing latitude and climatic severity invertebrate herbivores and large carnivores decline in species richness and abundance. Earthworms (Lumbricidae) are important only at the Soviet sites on the Taimyr Peninsula, in grassland (but not bog) habitats at Moor House and Glenamoy, and, possibly, at Stordalen.

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The dominant groups of tundra invertebrates are Nematoda, Enchytraeidae (Annelida), Acari, Collembola and Diptera. Acari, Collembola and Diptera are the only non-parasitic land arthropods on Antarctica (Gressitt, 1967). There are large variations in absolute and relative abundances between sites, and between habitats of any one site, and no clear pattern of abundance and biomass emerges. Enchytraeidae, Collembola and Diptera are frequently abundant across the full range of sites, particularly in wet to mesic habitats. Acari become more important in sub-arctic sites and in mesic to dry habitats.

Specific trophic functions cannot be assigned to the dominant invertebrate taxa. All taxa include species believed to feed directly upon plant litter and humus, and other species that feed upon microbial tissue (e.g. Addison, 1977). Overall, the microbial feeding habit appears to predominate amongst tundra invertebrates. Tundra faunas, in general, lack the large, litter-dwelling invertebrates which feed upon fresh litter, a role played by terrestrial isopods, millipedes and earthworms in other ecosystems.

Observed rates of decomposition

A wide range of techniques has been used to measure rates of decomposition of organic matter in tundra sites. Some methods were standardised between sites to allow direct comparison and others were designed to answer questions which were specific to individual sites. In this section we describe first the decomposition of the total organic matter estimated by respiration measurements in the field. The total carbon output is composed of losses from a variety of individual substrates (plant remains), the decomposition of which is then described from measurements of weight loss and respiration. However, the chemical composition of the naturally-occurring substrates varies considerably between sites, so the decomposition of standard substrates, particularly cellulose and barley straw, is used to provide comparisons of the decomposition potential over the range of tundra sites.

Total carbon loss

The output of gaseous carbon from the litter and soil integrates the losses from the variety of substrates in the site. The carbon loss can, at least in theory, be compared with the carbon fixed by primary production to indicate the extent to which the system is either accumulating or losing dead organic matter. In addition it provides a comparable measure of decomposition in different sites. Various methods of measurement of gaseous carbon have been used but their efficiency is unknown and none of them distinguishes between carbon derived from the breakdown of plant

remains and that produced by root respiration. Few independent measurements of root respiration were made in the tundra programme (Billings, Shaver & Trent, 1973) but various studies indicate that between one third and two thirds of the total respiration originates from living roots (Macfadyen, 1971; Minderman & Vulto, 1973). The simulation of carbon flux at Point Barrow indicates that root respiration accounts for 33–70 % of soil respiration (Bunnell & Scoullar, 1975).

The main results (see Table 19.3) show a wide range of carbon output, with respiratory losses in the Hardangervidda dry meadow and birch forest actually higher than estimated primary production, possibly as a result of root respiration. In the wet meadow at Hardangervidda and the peat sites at Stordalen mire and Moor House the difference between respiration and production indicates that organic matter accumulation is taking place. The losses at Hardangervidda wet meadow may be underestimates because methane output was not measured in this minerotrophic site but methane was measured at the mire sites where, especially at Moor House, there were very few roots of higher plants to complicate the interpretation. In the *Sphagnum*-dominated bog habitats at Moor House and the mire at Stordalen only about 20–50 % of the net primary production is estimated as being lost as gaseous carbon.

Table 19.3. *Losses of gaseous carbon estimated from field measurements of respiration at various tundra sites. The approximate length of the decomposer season (approximate period without snow cover) and of net primary production are given*

Site		Carbon loss ($g\ C\ m^{-2}$)	Season (d)	Primary production ($g\ C\ m^{-2}\ year^{-1}$)
Norway:	Hardangervidda[a]		*	
	Lichen heath	94	140	114
	Wet meadow	253	133	351
	Dry meadow	457	140	225
	Birch forest	689	154	328
Sweden:	Stordalen mire[a]			
	Ombrotrophic mounds	50		
	Ombrotrophic/minerotrophic	14	134	72
	Minerotrophic depressions	16		
UK:	Moor House blanket bog[b]			
	Sphagnum pools	61		197
	Sphagnum lawns	35	270	153
	Sphagnum hummocks	51		98
USA:	Point Barrow[c]			
	Meadow	159	85	130

[a] From Svensson, Veum & Kjelvik (1975).
[b] From Clymo & Reddaway (1971).
[c] From Bunnell, MacLean & Brown (1975).

Methane production was maximal in the waterlogged minerotrophic depressions on the Stordalen mire where it accounted for 45 % of the total carbon output while at Moor House about 12 % of the carbon loss from decomposition was methane in wet *Sphagnum* areas but only about one % in the drier hummocks. At Point Barrow artificially heated meadow soils evolved 46–65 % of their gaseous carbon as methane. Thus methane production is significant in some of the waterlogged organic soils but, in view of the widespread occurrence of reducing conditions, it is surprising that it is not more commonly recorded in tundra sites. It is possible that methane-oxidising bacteria in the soil surface mask the production of this product of anaerobic decomposition in the lower horizons.

The field measurements of total carbon loss in respiration have emphasised the diurnal pattern of decomposition and, in the analysis of seasonal variation within sites, have shown that temperature is a major factor controlling the rate of decomposition, with moisture being a subordinate factor. The temperature-related seasonal pattern is disrupted, however, at melt-off and possibly at the end of the season. A rapid rise in respiration at thaw is indicated by the results from Hardangervidda birch forest where, at the border of a melting snow patch, a carbon loss of 30 mg m^{-2} h^{-1} was measured under 15 cm of snow, 137 mg m^{-2} h^{-1} at the melting snow border, and 259 mg m^{-2} h^{-1} where the surface had been free from snow for 3 h. At the moss bank on Signy Island, cores taken at the time of rapid thaw showed a peak in respiration compared with cores taken earlier and later in the season, even though they were all measured at 10 °C. A clear thaw-related peak in respiration was not observed at Point Barrow although respiration did deviate from its close relation to temperature at the beginning of the season. The results from the Hardangervidda, Signy and Point Barrow sites suggest that the thaw causes rapid release of nutrients and exposure of new organic matter surfaces, which allows a sharp increase in microbial activity.

Decomposition of natural substrates

The output of gaseous carbon from the litter and soil represents the combination of losses from a variety of plant remains (leaves, stems, roots), animal faeces, the remains of the decomposer organisms themselves and humus. Overall carbon output from decomposition reflects the combination of substrates available and their specific rates of decomposition, and there is a large variation in rates measured within a climatic area or site (Fig. 19.3). Low values occur at all sites, reflecting the woody nature of much of the litter and locally unfavourable conditions. The highest rates of decomposition occur at the warm oceanic sites which have long active seasons, relatively high temperature sums, and abundant precipitation during sum-
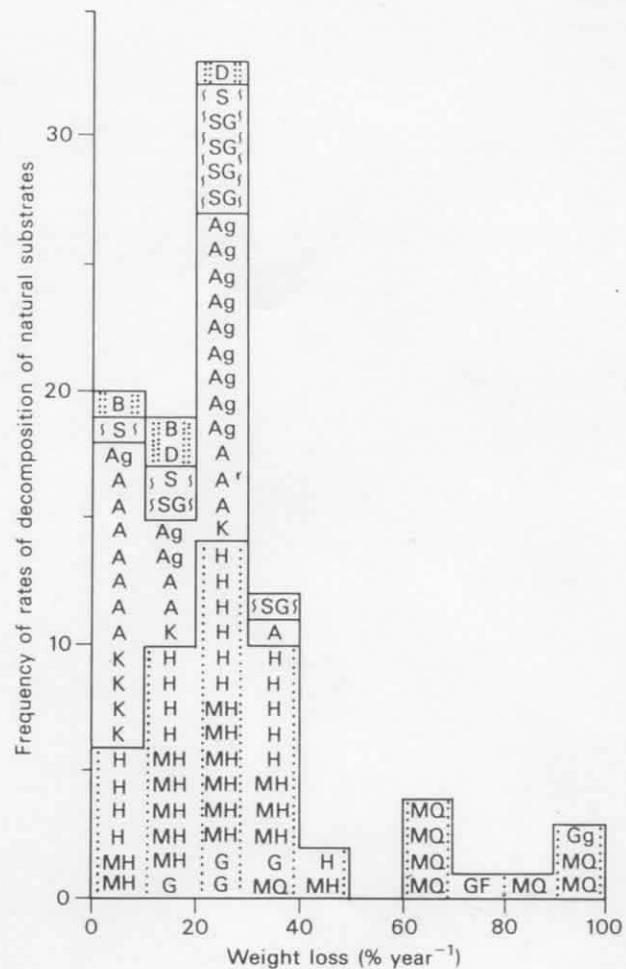
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Fig. 19.3. Frequency of rates of decomposition of natural substrates in a range of tundra sites (11 sites, 23 subsites). Data are for percentage weight loss in the first year of litters placed in the surface layers. Sites are grouped as cold continental ⬚⬚; cold oceanic ⟨ ⟩; warm continental ☐; warm oceanic ⟨ ⟩. Site initials are B – Point Barrow, D – Devon Island, S – Signy Island, SG – South Georgia, Ag – Agapa, A – Abisko Stordalen, K – Kevo, H – Hardangervidda, MH – Moor House, G – Glenamoy bog, GF – Glenamoy forest, Gg – Glenamoy grass, MQ – Macquarie Island.

mer. The only natural litters showing a greater than 50 % weight loss in the first year were at Glenamoy and Macquarie Island. Slower rates of weight loss occur on the dry Fennoscandian and Agapa sites – continental sites with short, warm and dry summers. The few data available from the polar sites show even lower loss rates. Of all habitats and litters, 75 % showed less than a 30 % weight loss in the first year of decomposition.

There is great variation in rate of decomposition of different litters within a site but the pattern is repeated in different sites. Woody stems and moss usually have loss rates of less than 10% per year while the losses from the most rapidly decomposing leaves are up to four to six times greater.

Many leaves remain attached to the plant within the sward for a year or more before they become incorporated into the litter layer. The microclimate of this standing dead material fluctuates more widely than that of the litter and it is difficult, if not impossible, to determine when losses through translocation and plant respiration cease and decomposer respiration begins. Indeed, the processes overlap within a single leaf. The limited information available indicates that the rate of decomposition of standing dead material may be similar to that of surface litters (Heal & French, 1974) although low moisture levels inhibit decomposition in the standing dead canopy at some sites, e.g. Point Barrow (Bunnell, MacLean & Brown, 1975). In contrast, the micro-environment of dead roots fluctuates less than that of the surface litter, but again the limited evidence indicates that their decomposition rates are similar (Heal & French, 1974; Rosswall, Veum & Kärenlampi, 1975).

Lemmings, reindeer, caribou, muskox and other herbivores contribute to the decomposer cycle by addition of faeces derived from live vegetation and some standing dead material. The faeces often retain their structural integrity for a number of years, e.g. for muskox dung, 1–3 years on the meadow and 3–11 years on the raised beaches at Devon Island (Booth, 1977). The results from Agapa (Vassiljevskaya *et al.*, 1975) indicate, however, moderate or high rates of decomposition with lemming faeces showing a weight loss of 24% per year and reindeer faeces losing 80%. Some of this loss may be through leaching and fragmentation, and respiration of lemming faeces at Point Barrow (Bunnell *et al.*, 1975) was 'of the same magnitude as from standing dead vegetation'.

Weight loss provides an integrated measurement of microbial and faunal respiration, leaching and loss of particulate matter. Only respiration is associated with catabolism of organic compounds and it is often used as a sensitive, short-term measurement of the influence of particular factors on the rate of decomposition of individual substrates (see later), and in detecting changes in decomposer activity with time. The sensitivity of respiratory processes to temperature and moisture conditions makes comparison of results obtained from various substrates difficult, especially when different research workers are involved. Taking heterotrophic respiration rates at 10 °C and at field moisture levels, the highest rates are of the order of 60–100 μl O_2 g^{-1} h^{-1} for decomposing leaves of *Rubus chamaemorus* at Stordalen and Moor House, *Carex aquatilis*, *Eriophorum angustifolium* and total litter at Point Barrow and *Carex stans* at Devon Island. Lowest rates were less than 20 μl O_2 g^{-1} h^{-1} for woody stems of *Calluna vulgaris* at Moor House, *Dryas* leaves at Devon Island and Eagle Summit and litter

from the lichen heath at Hardangervidda (Flanagan & Veum, 1974; Rosswall *et al.*, 1975; Widden, 1977). These respiration rates are broadly correlated with measured weight losses and the ranges are similar despite one measure being instantaneous and the other integrated over a year.

The influence of initial substrate quality on decomposition

The initial rates of decomposition of the substrates obviously vary considerably between plant species and between parts of the same species, as a result of variation in the physical and chemical characteristics of the substrate. There is no single measure of substrate quality. Leaching losses are influenced by the concentrations of soluble compounds and elements and by the presence or absence of a continuous water-resistant cuticle. Respiration by decomposer organisms relates to the relative amounts of substrates of different molecular size, to the availability of nutrients in the substrate and surrounding soil environment, and to the amount of surface area exposed to attack. In general, molecules of low molecular weight and simple structure are the first to be decomposed. Respiration, leaching and comminution by physical factors, fauna and microflora cause changes in the chemical and physical composition of the organic matter remaining. Bunnell, Tait & Flanagan (1977*b*) have shown for several tundra substrates that during the initial period of decomposition many of the changes in both substrate weight and chemical composition result from changing microbial respiration rates which are chemical-specific and independently influenced by temperature and moisture.

Some plant species accumulate inhibitory compounds, such as certain polyphenols, in their leaves. While selection of this characteristic probably relates more to resistance to herbivores than decomposers, the effect lasts after death, and such plants decompose slowly. We may expect plants with evergreen leaves which last several seasons to invest more of their resources in inhibitory compounds and in supporting tissue, including lignin. Thus evergreen litter is expected to decompose more slowly than deciduous litter and the inverse relationship between decomposition rate and lignin concentration may be enhanced by a positive association of lignin concentration with inhibitory compounds. This association has been observed in the evergreen leaves of *Dryas* (Bunnell *et al.*, 1977*b*).

Data from a number of tundra sites (Van Cleve, 1974) showed that differences in weight loss between litters are inversely related to the initial lignin concentration (Fig. 19.4). Lignin and cellulose are relatively resistant to microbial attack and there tends to be an inverse relationship between amounts of soluble carbohydrate and protein compared with the ligno-cellulose fraction. The rate of decomposition of the organic fractions is also dependent on the amount and availability of nutrients: there is a negative
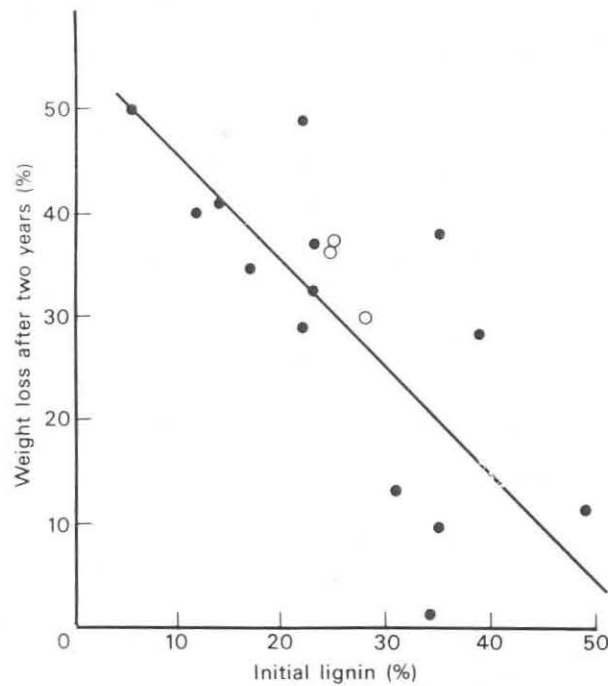
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Fig. 19.4. The relationship between percentage weight loss of litter after two years and the initial lignin concentration for litters at Point Barrow and Eagle Summit, USA (○), and Moor House, UK (●) ($y = 55.9 - 1.03x$). Data from Van Cleve (1974).

relationship of weight loss to the C:N ratio, a positive curvilinear relationship with potassium and calcium, but, surprisingly, no detectable relationship of weight loss with either nitrogen or phosphorus.

Limited data are available for litter respiration in relation to chemical composition but combining results from seven litters from Point Barrow and Moor House shows correlations between respiration and readily soluble carbon compounds (Fig. 19.5), lignin, nitrogen and potassium concentrations and no correlation of respiration with phosphorus.

Interpretation of the results on the influence of chemical composition on weight loss and respiration is confused because of the few data; variation in site conditions and in methods of chemical analysis; and intercorrelation of chemical variables obscuring causal relationships. In addition, the concentration of inhibitory compounds, such as certain polyphenols, can influence the rate of decomposition of other organic fractions. Thus, the observed inverse relationship of weight loss to lignin concentration probably represents a complex causal relationship involving amounts of (*a*) soluble organic fractions, (*b*) lignocellulose, (*c*) total and available nutrients, (*d*) inhibitory compounds, as indicated by the results from the weight loss
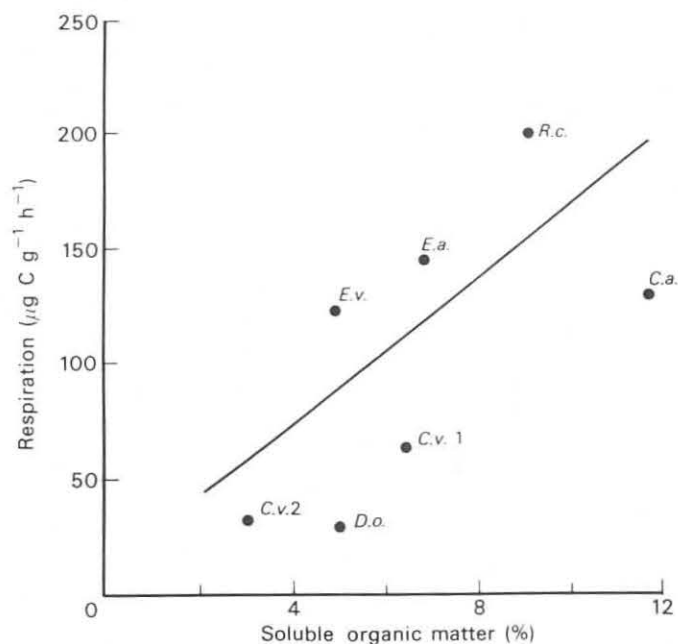
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Fig. 19.5. Respiration of litters in relation to the concentrations of readily soluble organic fractions. *R. c., Rubus chamaemorus*; *C. a., Carex aquatilis*; *E. a., Eriophorum angustifolium*; *E. v., Eriophorum vaginatum*; *C. v.* 1 *Calluna vulgaris* shoots; *C. v.* 2. *Calluna vulgaris* stems; *D. o., Dryas octopetala*; ($y = 13.9 + 14.0x$). Data from Flanagan & Veum (1974) and Heal *et al.* (1978).

and chemical analysis of 14 litters at Moor House (Heal, Latter & Howson, 1978).

The effect of the physical and chemical composition of the substrate on decomposition is clearly shown when fresh green litter enters the decomposer subsystem through clipping by herbivores. Such litter has relatively high concentrations of nutrients and soluble organic fractions and the initial rates of weight loss are up to five times higher than rates in litter of the same species which has died after resorption of soluble material (Bunnell, 1973; Heal & French, 1974; Widden, 1977).

Changes in substrate quality and decay rate with time

The relative rates of loss and resistance of the residual material produce decay–time curves that are characteristic of the initial substrate composition and environment (Minderman, 1968). At our present stage of understanding the decomposition of any litter can be represented by the combination of two negative exponential curves. The first defines the rapid loss of the more soluble compounds of low molecular size, the 'soft' fractions; the second

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defines the slow loss of the lignocellulose or 'hard' fraction (Fig. 19.6)
(Bunnell & Tait, 1974; Flanagan & Bunnell, 1976; Bunnell *et al.*, 1977*b*; Van
Cleve, 1974). Rapid loss of the soft fraction results from both leaching and
microbial respiration. Under laboratory conditions leaching can cause a
weight loss in litter equivalent to 95 % of the observed initial annual weight
loss of that litter in the field. The concentration of the leachable portion in
different age classes of live leaves and standing dead leaves of some tundra
plants (Fig. 19.7) shows that the bulk of the leachable fraction is removed
between senescence and early decomposition. This loss includes translo-
cation within the plant as well as respiration and leaching. Further change
in the leachable fraction is slight so that four-year-old leaf remains contain
a 4–6 % water-soluble fraction suggesting that leachates are generated as
recalcitrant fractions decompose. These potential leaching losses are very
similar to the observed weight losses under field conditions but the soluble
organic fraction is probably readily decomposed by microflora (Flanagan &
Bunnell, 1976; Bunnell *et al.*, 1977*b*).

The relationship between potentially leachable material and weight loss
and respiration does not show what proportion of field weight loss is
attributable to leaching and respiration. By using a model to calculate
respiration loss from temperature and moisture relationships, Bunnell &
Scoullar (this volume) estimated losses from respiration at 65–92 % of
observed weight loss, suggesting that leaching contributes 8–35 % of the
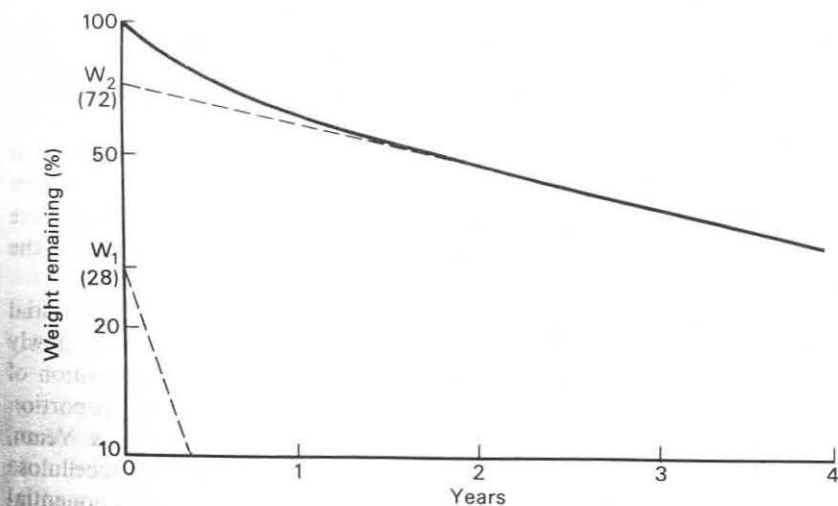

Fig. 19.6. Theoretical weight loss–time curve (——) for a litter, showing the component curves
(---) for rapid- and slow-decomposing components approximating to soluble carbohydrates
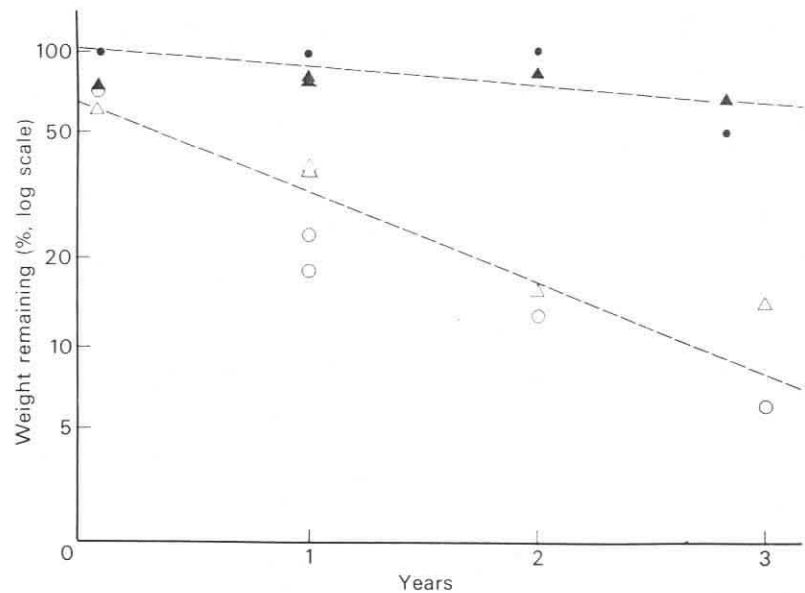and lignocellulose fractions with initial weights W_1 and W_2, respectively. From Bunnell & Tait
(1974).

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Fig. 19.7. Decay rates of organic fractions in litter at Point Barrow. Ethanol soluble fraction (△, *Carex aquatilis*; ○, *Eriophorum angustifolium*), non-ethanol soluble fraction (▲, *Carex aquatilis*; ●, *Eriophorum angustifolium*). From Bunnell *et al.* (1975).

field weight loss. An alternative estimate, based on estimates of leaching process characteristics (Bunnell & Scoullar, this volume), indicates that leaching losses for four litters were less than 5% per year. These estimates suggest that leaching is a small component of weight loss in fallen field litter. In contrast, Widden (1977) found that more weight loss occurred during the winter than during the 90-d growing season on Devon Island; the loss was attributed to leaching during spring melt. Weight losses due to respiration and to leaching may well be complementary, since the water-soluble fraction is also readily decomposed by microflora, in which case the ratio of losses due to leaching and to respiration is unimportant to the overall loss rate.

Litters with high concentrations of soluble compounds have high initial respiration rates which decline with time more markedly than in slowly decomposing litters. The decline reflects the more uniform composition of the slowly decomposing litters, and the increase with time in the proportion of lignocellulose in the rapidly decomposing material (Flanagan & Veum, 1974). Thus in organic matter containing a high proportion of lignocellulose the fraction remaining approximates closely to a single negative exponential curve, while with increasing proportions of soluble organic fractions the two components of the decay–time curve become more distinct (Bunnell & Tait, 1974).

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The decay-time curves portray the amount of a particular initial sub-strate remaining, over time. The actual decomposition rate at any site integrates over the array of substrates available for decomposition, at any point in time. This is determined by the characteristics of fresh litter, its rate of change with time and the time-course of input of fresh litter. In the schematic representation of Fig. 19.8 (recognising that substrate quality cannot actually be ordered along a single axis), the composition and quantity of different categories of fresh litter determine initial substrate quality, Q_0, while the change in quality, dQ/dt, is determined by site-specific characteristics of temperature, moisture, etc. influencing the decomposition process. The array of substrates available at any time, t_i, is determined by both initial quality, Q_0, and dQ/dt. Particularly where there is a slow rate of decompositon, the remains of old organic matter may accumulate relative to fresh litter, contributing to humus formation.

There are no direct measurements of the rate of decomposition of the organic matter left after the early stages of decomposition described above, but the radiocarbon dating on a number of sites shows that organic matter in the lower parts of the profiles is often more than a thousand years old (Douglas & Tedrow, 1959; Bliss, 1975; Collins, Baker & Tilbrook, 1975). In
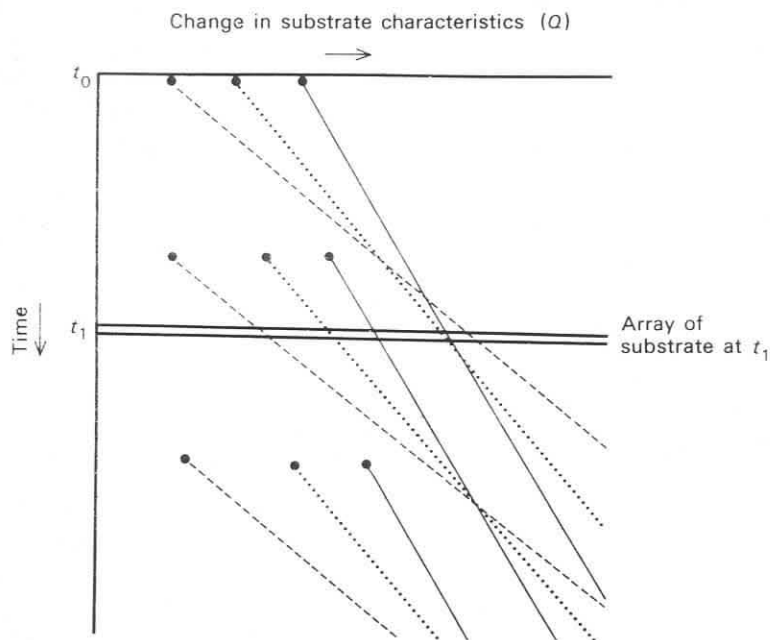

Fig. 19.8. Schematic representation of the change in substrate characteristics (Q) of a number of litters with time (t), indicating the array of substrates available to decomposer organisms at any given point in time, e.g. t_1.

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sites with permafrost the organic matter, as it moves down the profile, or is deposited as root remains within the profile, has an increasingly restricted active season until it is incorporated into the permafrost where decomposition ceases. The anaerobic conditions in some sites, resulting from waterlogging, also increase with depth and severely restrict the later stages of decomposition. In particular the fungi capable of degrading compounds of large molecular weight, which are relatively more abundant in older substrates, are inhibited by low levels of oxygen. Thus the disintegrated plant remains and amorphous humus are both biochemically resistant to decomposition and are in an inhibitory environment. In the anaerobic zone of the blanket peat at Moor House, estimated rates of decomposition range from 5×10^{-3} to 4×10^{-8} g g^{-1} year^{-1} (Clymo, 1978).

Although we have emphasised the variation in the chemical composition of the substrates, both between litters and in the same litter over time, it is recognised that the physical structure of substrates is also variable and influences the rate of decomposition through its effects on moisture-holding capacity, oxygen diffusion and on availability of surfaces for attack by micro-organisms (Bunnell & Tait, 1974). The succession of micro-organisms and fauna on litter as it decomposes is caused partly by changes in physical structure. The feeding action of invertebrates exposes fresh surfaces for microbial attack and probably accounts for the increase in microbial respiration and litter weight loss with increasing populations of enchytraeid worms at Moor House (Standen, 1978) and Collembola at Devon Island (Addison, 1977). It is significant that the litter-feeding species of Collembola had more effect on microbial respiration than did a fungus-feeding species. The absence of large litter-feeding invertebrates from tundra sites probably reduces the rates of comminution compared with other biomes and also limits the extent to which litter and soil are mixed and anaerobic pockets are disturbed.

Decomposition of standard substrates

Superimposed on any pattern of decomposition resulting from climatic and edaphic factors is a considerable variation owing to substrate quality. Measurement of standard substrates in a range of sites removes the effect of substrate quality and provides a means of comparing the decomposition potential of the sites. Some plant species occur at a number of sites and measurement of the rate of decomposition of these (Table 19.4) provides an assessment of the inter-site variation. The interpretation is limited, however, by variation in the initial state of the litter and by comparability of methods. With the exception of Eagle Summit, which is an alpine site, the sites are eutrophic or oligotrophic mires in warm continental or warm oceanic climates. The range for these mires is less than three-fold, but the

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Table 19.4. *Decomposition of comparable litters over a range of tundra sites. The data are percentage weight loss in the first year unless otherwise stated. (From Heal & French, 1974)*

Litter type	Stordalen	Moor House	Glenamoy	Sivaya Maska	Petchora	Lammin-Suo	Eagle Summit
Rubus chamaemorus	16-32[a,b]	36-38[a]		36[c] (9 months)	57[c]	35[c]	
Eriophorum vaginatum	—	22-26[a]	20		43[c]	24[c]	5-6[b]
Betula nana	21-30[a]	—	—	32[c] (9 months)	31[c]		

[a] The range for different years.
[b] The range for different methods.
[c] Mean values for subsites.

result from Eagle Summit indicates that the addition of polar and alpine sites would greatly increase the variation. At Hardangervidda a standard barley straw litter was placed on each of the five study sites within the same macroclimatic zone. The biological, chemical, physical and microclimatic differences between the soils of these sites produced a nearly four-fold range of weight loss in the first year: lichen heath, 10%; wet meadow, 20%; snowbed, 23%; dry meadow, 25%; birch forest, 38% (Rosswall *et al.*, 1975).

A clearer indication of the variation due to climatic and edaphic conditions is given by the rates of decomposition of two types of cellulose which were distributed between the IBP tundra sites (Heal, Howson, French & Jeffers, 1974; Rosswall, 1974). The decomposition of Borregaard cellulose pieces (Fig. 19.9) and cotton strips (Fig. 19.10) confirms the general pattern indicated by the natural litters (Fig. 19.3). Consistently low annual losses occur in the cold continental and cold oceanic sites compared to higher rates, with a wide range, in the warmer continental and oceanic sites. Given non-waterlogged and nutrient-rich conditions the rates in the temperate sites may be 10 times higher than the highest in the polar sites.

The cotton strips are placed vertically in the soil profile and in Fig. 19.10 the results for the first 4 cm of soil are given. In this respect they reflect the influence of soil conditions rather more than do the natural litters and Borregaard cellulose which were placed on or in the surface litters. Analysis of variance of the cotton strip data for 21 subsites indicated that variation due to microhabitat conditions such as moisture accounted for about 5% of the total variation (Table 19.5). A similar analysis of loss rates from natural litter (Table 19.5) showed, surprisingly, that within-site variation accounted
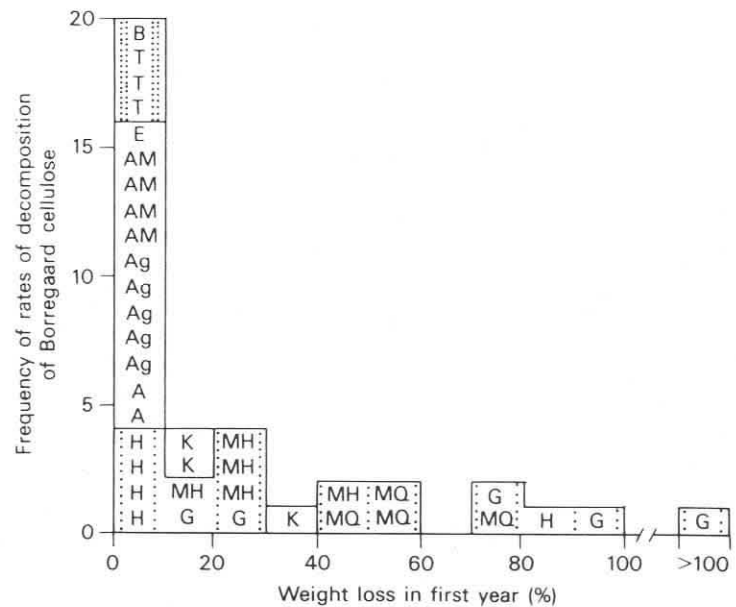
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Fig. 19.9. Frequency of rates of decomposition of Borregaard cellulose in a range of tundra sites (11 sites, 34 subsites). Sites are grouped as cold continental [⠿ ⠿]; warm continental [☐]; warm oceanic [⠂ ⠂]. Site initials as in Fig. 19.3, plus T – Tareya, E – Eagle Summit, AM – Ary-Mas. Data from Rosswall (1974).
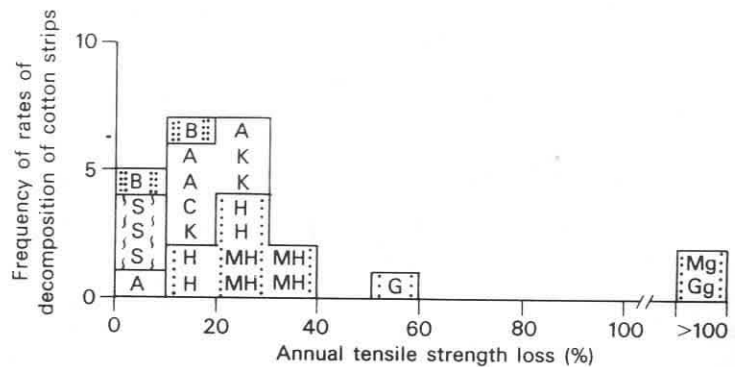

Fig. 19.10. Frequency of rates of decomposition of cotton strips in a range of tundra sites (7 sites, 23 subsites). Decomposition is measured by the annual loss in tensile strength, in kg, compared with the tensile strength of control strips (25–28 kg). Rates are adjusted to loss in one year. 100 % loss in tensile strength approximates to a weight loss of 20–25 %. Sites are grouped as cold continental [⠿ ⠿]; cold oceanic [⠈ ⠈]; warm continental [☐]; warm oceanic [⠂ ⠂]. Site initials as in Fig. 19.3. Data from Heal *et al.* (1974).

for only 8 % of the total variation, indicating that substrate quality added little to the microhabitat variation. However, further examination showed that the litter analysis was very strongly influenced by data from Macquarie

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Table 19.5. *Analysis of variance of the within- and between-site variation in the first-year loss in tensile strength of cotton strips and of weight loss of litters. Data from Heal & French (1974); Heal et al. (1974)*

	Degrees of freedom	Sum of squares	Mean square	*t*
Cotton strip (0–4 cm)				
Within-site	168	8201	49	
Between-site[a]	20	21 112	1056	21.6***
Litters				
Within-site	70	9579	137	
Between-site[b]	12	20 129	1677	12.26***
Litters (excluding Macquarie Island)				
Within-site	63	7193	114	
Between-site	11	2539	230	2.02*

[a] At Point Barrow, Signy Island, Kevo, Stordalen, Hardangervidda, Moor House and Glenamoy.
[b] At Point Barrow, Signy Island, Stordalen, Hardangervidda, South Georgia, Macquarie Island, Moor House and Glenamoy.

***$P < 0.001$; *$P < 0.05$.

Island, a warm oceanic site with a limited range of litters having intrinsically high decay rates. When the Macquarie data were excluded from the analysis, still leaving a range of sites equivalent to that used for the cotton strips, the within-site variation accounted for about 30% of the total variation, and between-site differences were significant only at the $P < 0.05$ level. The within-site variation is probably not fully expressed in the results because the more resistant woody litters were not sampled at some sites. However, the evidence emphasises that, even over this wide range of sites the variation in decomposition resulting from variation in substrate quality within the sites may be almost as great as that resulting from between-site conditions.

Decomposition in relation to environmental factors

The observed decay rates of natural and artificial substrates described above are the integrated response of the microflora and fauna to the combined effects of substrate composition, climate and soil conditions. It is possible to detect, from inter- and intra-site comparisons of field data, the influence of a number of factors on decomposition and decomposer populations. These factors often interact with each other.

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Temperature

The observed annual percentage weight losses of litters (y) under field conditions are weakly correlated with site temperature (x), as expressed by heat sum

$$y = 0.58 + 0.01x \quad (r = 0.32, \; n = 74, \; P < 0.01)$$

The correlation could not be strong because of the wide range of rates occurring within a single climatic site, the influence of other factors and non-linearity in the temperature–decomposition rate relationship. The effect of litter quality is eliminated by use of a standard substrate. The correlation of cellulose percentage weight loss in the first year with heat sum

$$y = 1.91 + 0.02x \quad (r = 0.44, \; n = 40, \; P < 0.01)$$

shows some increase in the amount of variation explained by temperature. The regressions suggest that, over the range of temperature conditions included in the biome, weight losses vary three- to six-fold because of temperature variations.

From respiration measurements of a range of litters from different sites (Fig. 19.11) over the temperatures normally occurring in tundra, we may generalise that:

(1) respiration is positively related to temperature over the approximate range $-5\,°C$ to $25\,°C$;
(2) at the lower end of the curve ($-5\,°C$ to about $+10\,°C$) the curve is approximately exponential with $Q_{10} = 3.5$–4.0;
(3) as temperature approaches the respiration maximum at about $25\,°C$ the relationship differs significantly from the exponential, and calculated Q_{10} falls.

These respiration–temperature characteristics represent the combination of responses from individual species populations of micro-organisms and fauna. Although the species of microflora show varying temperature ranges and optima (Fig. 19.12) the combined populations produce a uniform response curve. Over the range of temperatures which occur as a result of diurnal and seasonal variations, there is a succession of organisms adapted to prevailing conditions. Microbiological studies have shown that many isolates from tundra sites can be classed as psychrophiles and have the potential for activity at sub-zero temperatures. This is corroborated by measurements of litter respiration both in the laboratory and in the field (e.g. Svensson, Veum & Kjelvik, 1975). Sub-zero activity is indicated at the warm oceanic as well as at the polar sites. The physiological tests of a large number of bacterial isolates from various sites showed that less than 20 % of the bacteria from Stordalen, Moor House and Glenamoy grew at $+2\,°C$
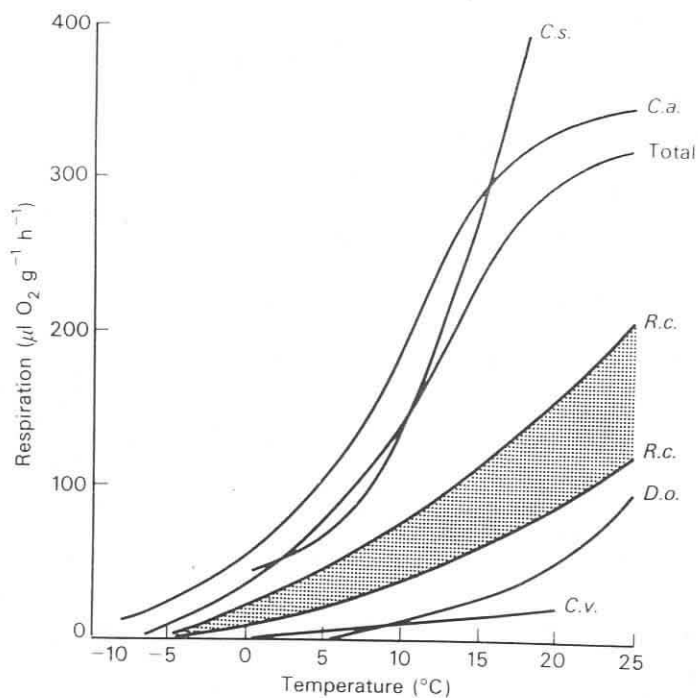
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Fig. 19.11. Respiration rates of a variety of litters in relation to temperature. *C. s., Carex stans*; *C. a., Carex aquatilis*; *R. c., Rubus chamaemorus*; *D. o., Dryas octopetala*; *C. v., Calluna vulgaris* stems; total = total litter at Point Barrow. The range of rates observed for *Rubus chamaemorus* litter in different years and at Stordalen and Moor House is shaded. Data from Flanagan & Veum (1974), Bliss (1975) and Rosswall *et al.* (1975).

as compared with more than 80 % from Hardangervidda and 50–70 % from temperate sites (Rosswall & Clarholm, 1974; Holding, this volume).

Respiration rates of invertebrates are normally measured on single individuals or, at most, a few individuals of the same species and size, isolated from their normal substrate. Under these conditions, respiration rate increases over the range of temperature normally encountered by the organism and tends to be linear rather than exponential. The upper temperature limit for respiration of tundra invertebrates has not been defined but unpublished results of S. F. MacLean and L. E. Clement showed erratic respiration, suggesting that temperature was nearing lethal levels at 20 °C for two species of craneflies (Diptera: Tipulidae) from Point Barrow. At +0.5 °C the respiration rate of these two species was approximately 40 % of the rate at 10 °C. Linear extrapolation of invertebrate data indicates that respiration of some arthropods may cease at temperatures just above zero but continues to well below zero for others (e.g. Hofsvang, 1975; Steigen, 1975). Linear extrapolation will underestimate respiration
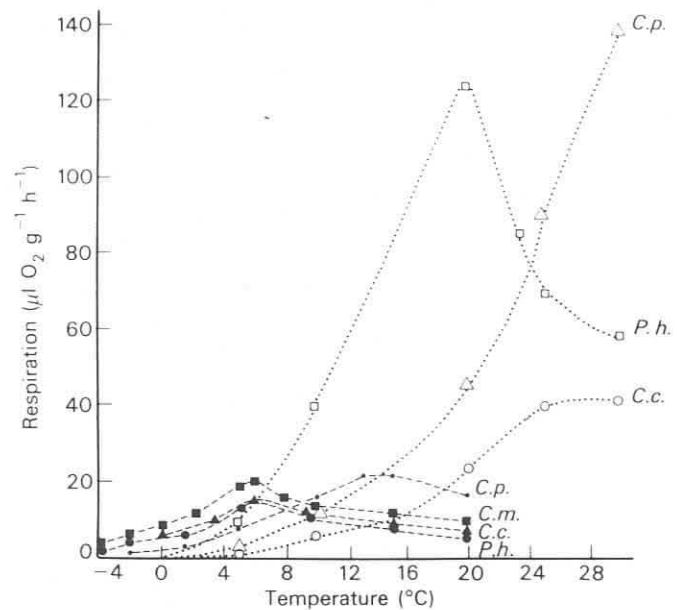
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Fig. 19.12. Respiration of a range of fungal isolates from Point Barrow in relation to temperature and substrate (solid symbols, cellulose; open symbols, pectin). *C. c.*, *Cladosporium* cf. *cladosporoides*; *P. h.*, *Phialophora hoffmanni* (group); *C. p.*, *Chrysosporium pruinosum*; *C. m.*, *Cylindrocarpon magnusianum*. From Flanagan & Scarborough (1974).

rate at low temperature if the respiration–temperature relationship tends toward the exponential. However, there appear to be marked differences in the respiration response of soil invertebrates compared with that for the microflora.

Taking the respiration–temperature curve for total litter at Point Barrow (Fig. 19.11), the distribution of respiration values in different temperature ranges calculated from the daily mean temperatures showed that although respiratory activity occurs at low temperatures it contributes little to the annual respiration. A high proportion of annual decomposition is contributed by the 30 % of days on which temperatures are relatively high. A similar calculation which uses temperatures recorded at two-hourly intervals gives daily respiration as being 12 % higher than that calculated from mean daily figures, emphasising the importance of short periods of high temperature (Bunnell & Tait, 1974). At most tundra sites summer temperatures range between 5 and 15 °C; at these temperatures the respiration rate is highly sensitive to small changes in temperature (Fig. 19.11).

Using the respiration–temperature curve for total litter at Point Barrow, and assuming optimal moisture conditions, the seasonal respiration pattern and annual litter weight loss have been calculated from

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the monthly mean air temperatures for a number of sites in the Tundra Biome. The results for selected sites (Fig. 19.13) show the varying influence of both length and warmth of the summer. For example, Macquarie Island shows a long period of medium respiratory loss compared with continental sites such as Tareya and Kevo with short seasons, but varying maximum temperatures. The relative contribution of length and warmth of the summer to the annual weight loss of litter is shown in Fig. 19.14. Thus similar potential weight losses are predicted for Signy Island (15%) with a long cool summer and Devon Island (17%) with a shorter but warmer

Fig. 19.13. Potential respiration derived from the respiration-temperature curve for total litter at Point Barrow (at optimal moisture) for selected tundra sites based on site temperature data Arctic (——) and antarctic (– – –) sites.
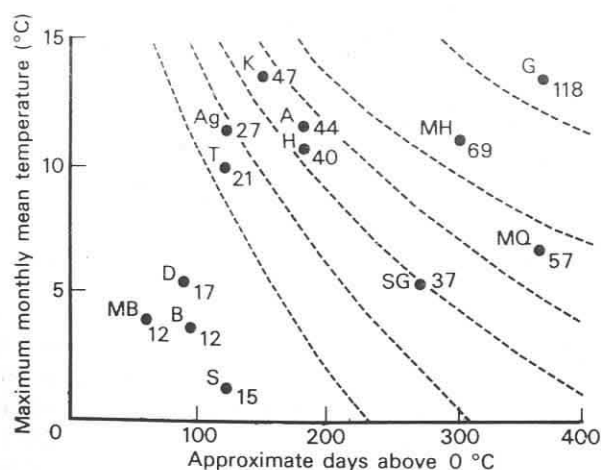

Fig. 19.14. Annual weight loss of litter estimated from curves derived as in Fig. 19.3, shown in relation to the site temperature regime. Approximate isolines of weight loss are indicated. Site initials are as in Fig. 19.3 plus T – Tareya, MB – Maria Pronchitsheva Bay.

summer. South Georgia (37 "„) and Stordalen (44 "„) also show the complementary effect of oceanic and continental conditions. Approximate isolines of weight loss are given (Fig. 19.14) but it must be emphasised that they are for litter of the type found at Point Barrow and the effect of moisture, as discussed in the following section, is not incorporated into these calculations. However, the predicted values correspond reasonably well with the higher observed loss rates at each site (Fig. 19.3). The main deviations are explainable by either very wet (Glenamoy and Moor House) or dry (Kevo) conditions where predicted values are higher than observed values. The predicted weight loss for Macquarie Island is lower than the observed losses, possibly as a result of high substrate quality. In addition, the effect of temperature is modified by selection for micro-organisms able to grow at low temperatures (Flanagan & Scarborough, 1974; Rosswall & Clarholm, 1974; Holding, this volume).

Some of the within-site variation is also attributable to temperature. Minor changes in topography, vegetation cover and soil aeration can produce variations of $\pm 10\%$ of the mean site temperature at any time. In general, microsites with daily maxima higher than the site average also have lower daily minima than the site average. The greater variation, which is also characteristic of alpine compared with polar tundra, results in higher rates of decomposition, although there may be relatively little difference in mean temperatures or in the temperature sum. Dry sites and microsites have greater temperature fluctuations in the litter and soil than wet sites under the same climatic regime. Thus at Devon Island the degree-day accumulation at 5 cm in the soil was 2.2 to 4.9 times greater in the dry beach ridge than in the wet meadow soils. Again we are back to two of the dominant themes in this paper: the importance of within-site variation and the interaction of environmental factors.

Moisture

The range of moisture conditions in organic horizons of the Tundra Biome sites (Fig. 19.2) is very wide. In many sites moisture levels in the surface layers are commonly sub-optimal for decomposition because of low precipitation, good drainage or high evaporation during the summer. There is a second group of sites in which moisture levels are generally optimal for decomposition (approximately 200–500%) and in some wet sites drying during the summer brings moisture into the optimum range. A third group of sites has high moisture levels which tend to inhibit decomposition, particularly in deeper parts of the profile.

The distribution of weight loss values for various litters when grouped according to site moisture supports this interpretation (Fig. 19.15). At sites with low moisture levels, decay rates are consistently low. At sites with high
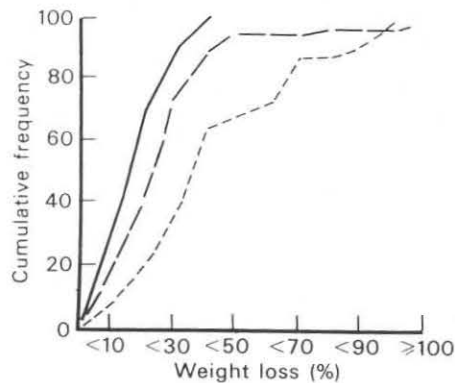
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Fig. 19.15. Litter weight losses in the first-year in dry (——), mesic (— — —) and wet (— · — · —) tundra sites. The curves are cumulative frequency for each site type against percentage loss. From Heal & French (1974).

moisture levels, decomposition rates are slightly higher, with the exception of two very high values (70% and >100%) at Glenamoy forest and grassland. Litters at mesic sites show the highest rates and considerable variation.

When the observed field rates of decomposition are compared with the moisture status of the sites, using the median moisture value for each site, there are very poor correlations. This may be attributed to:

(1) the existence of a broad moisture 'optimum' for decomposition, within which other factors have the greatest effect on rate;
(2) the rates being influenced more by the magnitude and duration of moisture excursions to high and low values than by median moisture levels;
(3) the non-linearity of the response to moisture, with both high and low values being inhibitory, as shown in Figs. 19.15, 19.16 and 19.17;
(4) the expression of moisture as a percentage of dry weight.

The response of respiration to variation in moisture may be poorly expressed by gravimetric measures of moisture in some substrates (Bunnell, Tait, Flanagan & Van Cleve, 1977a). In a soil or litter with small pore size waterlogging occurs at much lower moisture contents than when pore size is large. Douglas & Tedrow (1959) showed that maximum decomposition rates in an arctic brown soil at 19.5 °C occurred at about 50% moisture content while with an upland tundra soil it occurred at 30%. 'The arctic brown soil (on a beach ridge) is much coarser textured and, with more and larger pores, the waterlogging effect does not manifest itself until there are large quantities of moisture present.' These soils contained 13–14% organic matter. The optimum moisture for respiration in a peaty high-centre
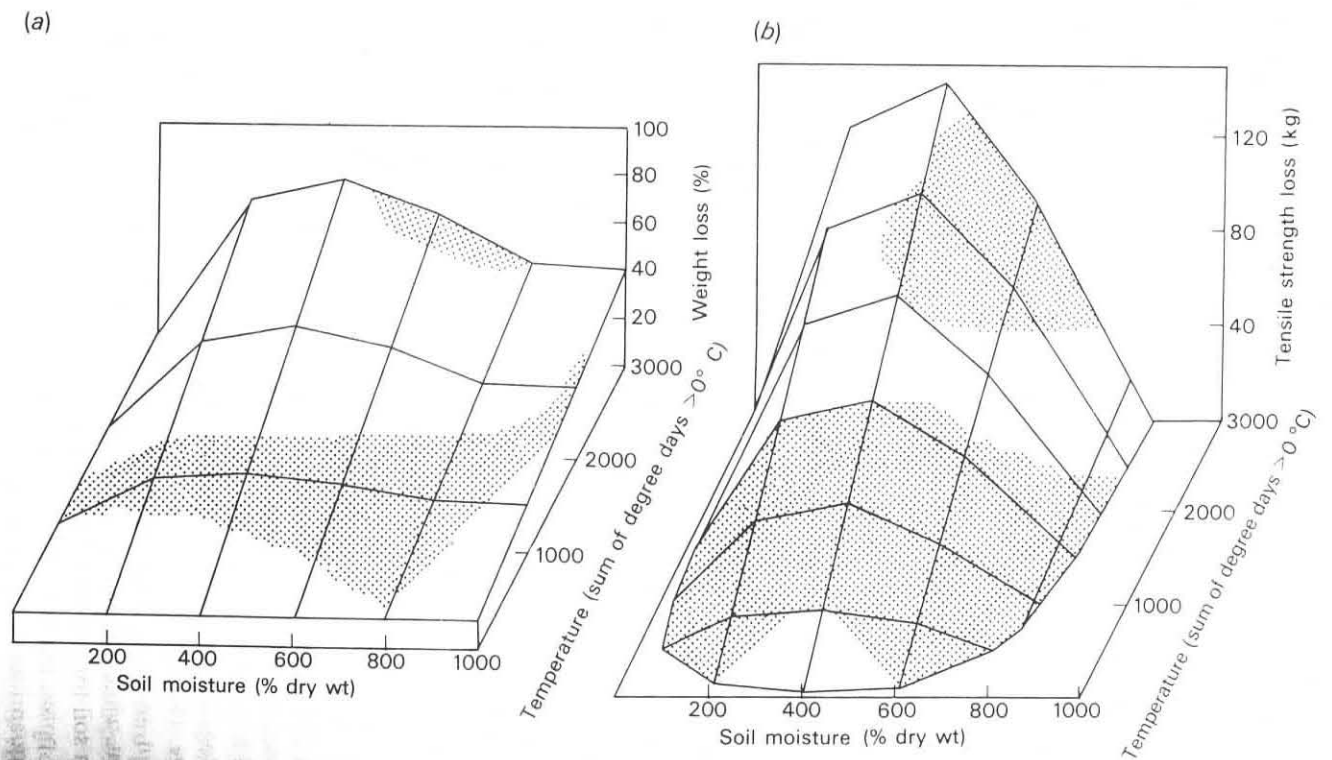
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(a)

(b)

Fig. 19.16. (a) Maximum first-year weight loss of litters and (b) tensile strength loss of cotton strips at 0–4 cm as a function of site temperature and soil moisture. Shaded areas show the actual distribution of data over the response surface. From Heal et al. (1974) and Heal & French (1974).
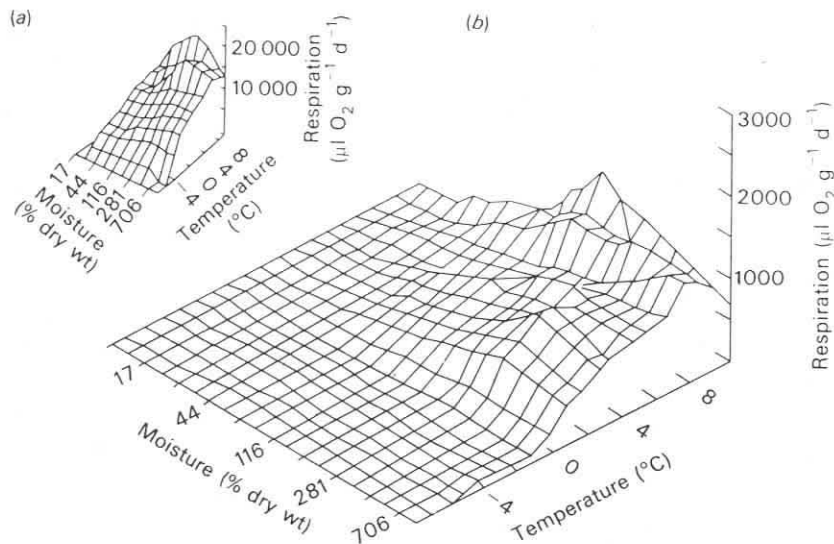
Fig. 19.17. Respiration (*a*) of one-year-old dead leaves of *Eriophorum angustifolium* and (*b*) of total site litter at Point Barrow as a function of temperature and moisture. From Flanagan & Veum (1974).

polygon was about 70 % and in a half bog was about 500 %, these soils containing 37 and 67 % organic matter, respectively. Thus it is the moisture-holding capacity and the degree of saturation of the soil which is important in determining the influence of moisture and in comparing different sites, particularly when comparing organic and mineral soils. Estimation of the moisture content at saturation at the Hardangervidda sites indicated that 60–80 % of saturation was optimal for soil respiration in organic rich soils, corresponding to moisture contents of 200–500 % (Flanagan & Veum, 1974). Data are inadequate to allow a detailed analysis of moisture saturation and decomposition across national sites. Bunnell *et al.* (1977*a*) demonstrated the sensitivity of microbial respiration to moisture in natural substrates from Point Barrow and noted that moisture accounted for 23–31 % of the variation in different soil layers of an aspen boreal forest.

Inhibition of decomposition resulting from dryness is a regular seasonal feature in some warm continental sites, such as Kevo and Stordalen (Kärenlampi, 1971; Rosswall *et al.*, 1975), and in well-drained habitats of high arctic tundra (Widden, 1977). The surface layers can dry to such an extent that decomposition almost ceases, even though the site may be very wet at other times of the year; thus the Stordalen site may pass from inhibition from excess moisture to inhibition from insufficient moisture over the course of a season. The more stable moisture content in lower layers

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probably maintains activity throughout the summer (Van Cleve & Sprague, 1971). In the birch and pine sites at Kevo, decomposition of cellulose at 3–10 cm is about twice that at the surface (Rosswall, 1974).

In very wet sites, especially those at the warm end of the Tundra Biome, decay rates decline markedly with depth. In peat sites (Glenamoy, Moor House and Stordalen) decay rates at 10–20 cm may be only 20 % of those at the surface, despite a relatively flat temperature profile in the peat (Heal & French, 1974; Heal *et al.*, 1974; Rosswall, 1974; Berg, Kärenlampi & Veum, 1975). This is related to the development of reducing conditions (anaerobiosis) in waterlogged soils. Reducing conditions may develop more easily in warm sites, since biological oxygen demand increases with temperature more rapidly than does the oxygen diffusion rate.

Measurements of the rate of respiration of organic matter under varying moisture levels in the laboratory and field show broadly similar relationships, despite the variation in respiration resulting from differences in substrate quality (Flanagan & Veum, 1974). For a wide range of litters and organic horizons there is a direct, almost linear, relationship of respiration to moisture over the range 20–200 % moisture as shown in Fig. 19.17. Optimum conditions occur rather broadly over the range 200–600 % moisture, with a tendency for litter to show a more distinct moisture optimum than older organic matter, where there is more of a plateau (Flanagan & Veum, 1974). There is usually a decline in respiration at higher moisture levels but this has not been observed in some litters at Stordalen, Glenamoy and Moor House (Flanagan & Veum, 1974; Heal *et al.*, 1978; Rosswall *et al.*, 1975).

The decline in respiration at high moisture levels results from the development of anaerobic conditions, and artificially induced high oxygen levels prevent the decline (P. W. Flanagan, personal communication). The relatively sharp decline in respiration in fresh litters may result from high respiration rates causing the more rapid development of anaerobic conditions in comparison with older material with relatively low rates of respiration.

There is some evidence that oxygen uptake and carbon dioxide release can rise under extremely wet conditions, i.e. at moisture levels above about 1000 %. This probably results from the growth of water moulds and from an increase in fermentation processes. Respiration rates of individual species of fungi increase with increasing moisture levels above about 20 %. Above about 400 % some species show a decline in respiration, while others show continued increase up to at least 2000 %, or essentially aquatic conditions (Flanagan & Scarborough, 1974). Data on the growth and respiration response of invertebrates to moisture are lacking but differences in the species and higher taxon composition of the fauna are often related to between-habitat and between-site differences in soil moisture. As for

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microbial populations, greatest faunal densities and biomass occur on mesic sites and habitats while at waterlogged sites such as Point Barrow and Moor House anaerobic conditions are probably an important factor influencing faunal distribution and abundance (Coulson & Whittaker, 1978).

In the lichen heath habitat at Hardangervidda a midsummer reduction in the oribatid mite population is attributed to aestivation of a part of the population in response to drought (Solhøy, 1975). However, our present understanding suggests that soil moisture is more important in determining the abundance and composition of invertebrate faunas than it is in directly influencing rates of activity of the organisms present. The replacement of one species by another along the moisture gradient probably minimises the effect of moisture upon community function except under very dry or anaerobic conditions.

Temperature and moisture combined

The field results for the annual decomposition of litters and cotton strips over the range of tundra sites when plotted against the site temperature (sum of degree days above 0 C) and soil moisture (mean percentage of dry weight) produced a characteristic temperature–moisture 'hump' (Fig. 19.16). Rates of decomposition rise with increasing site temperature and are maximal when soil moisture is at about 400 %, rates being inhibited both above and below this moisture level.

A more precise response surface (Fig. 19.17) is derived from measurements of litter respiration under a wide range of controlled combinations of temperature and moisture content. The surface does not show a symmetrical peak, as would result from a simple multiplicative model, but a somewhat elongated and diagonal ridge, with the optimum moisture level decreasing as the temperature increases. This asymmetry probably results from the balance of rates of oxygen consumption by micro-organisms and the diffusion of oxygen from air to the water in the substrate. As the temperature rises, oxygen consumption increases but the diffusion rate does not increase so rapidly, thus oxygen limitation occurs at lower moisture levels. This asymmetrical 'hump' has been demonstrated for several types of litter and appears to have widespread application, with the additional effect of the height of the surface being raised or lowered by substrate quality (Douglas & Tedrow, 1959; Bunnell & Tait, 1974; Flanagan & Veum, 1974; Flanagan & Bunnell, 1976; Bunnell & Scoullar, this volume).

Examination of the seasonal variation in respiration within sites indicates that, in general, temperature controls much of the variation. In the five sites at Hardangervidda, temperature accounted for 64–81 % of variation in respiration. Moisture had a significant effect only in the lichen heath and snowbed sites where it accounted for only 4 % of respiration but contri-

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buted significantly to the combined regression (Svensson *et al.*, 1975). In Alaska, at Point Barrow and in the taiga near Fairbanks, moisture influenced respiration less than did temperature (Douglas & Tedrow, 1959; Flanagan & Veum, 1974, Van Cleve & Sprague, 1971). Although the relationship between temperature and moisture is complex, simulation models relating microbial respiration to these factors account for 71–90% of the variation in a wide variety of tundra and taiga substrates (Bunnell *et al.*, 1977*a*).

The combined effects of climate and soil conditions

Although temperature may appear to be the dominant factor which varies over the Tundra Biome, multivariate analyses of climate and soil characteristics of the IBP sites showed them to be distributed along a number of complex axes representing intercorrelations and interactions of site variables (French, 1974). Two of the axes reflect factors which might be expected to influence decomposition: Component I of Fig. 19.18 represents trends from cold, dry, alkaline mineral soils low in nitrogen to warm, wet, acid, organic soils with higher nitrogen contents; Component IV represents trends from acid, mineral, low-phosphorus soils to more alkaline, organic, high-phosphorus soils. When rates of decomposition of litters or cellulose are plotted along these two component axes a diagonal increase in rate appears as shown in Fig. 19.18 (Heal & French, 1974; Heal *et al.*, 1974).
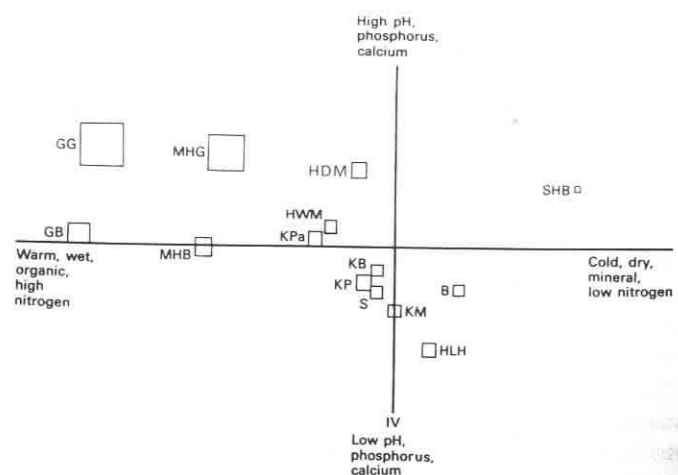

Fig. 19.18. Annual loss in tensile strength of cotton strips in the surface 0–4 cm superimposed on axes derived from Principal Components analysis of site climate and soil data. The areas of the squares are proportional to the loss in tensile strength. Site initials as in Fig. 19.2, plus GG – Glenamoy grassland. Data from Heal *et al.* (1974).

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Regression of the loss rates against the component values and against specific soil and climatic variables indicated that litter quality is the most important factor influencing decay rates. The relative importance of soil conditions compared with climate is difficult to assess because many soil variables such as pH and nitrogen concentrations are highly correlated with temperature and moisture variables. However, the availability of soil phosphorus and calcium are not closely correlated with climate and therefore provide an independent measure of soil nutrient status. In a number of analyses temperature and moisture accounted for about 60 %, of the variation in decay rate and the addition of soil nutrient variables increased this to 80–90 %. The relationships were shown to be non-linear and interactive, with climatic variables increasing in importance relative to soil nutrients as litter quality improves, probably reflecting the degree of dependence of the decomposer microflora on the nutrients in the soil rather than in the litter. Thus the range of variation in one environmental variable can affect the extent to which other variables influence decomposition.

Van Cleve (1974) distinguished the quality of incoming organic matter, or secondary substrate, from that of the primary substrate – the soil and its associated organic matter. The properties of a soil which affect the capacity of the decomposer system to break down introduced organic matter include acidity, the concentrations and relative proportions of mineral cations and anions, organic and inorganic nitrogen, and various organic fractions. Although it has long been recognised that this complex of soil factors influences decomposition and decomposer populations, our understanding of the mechanisms involved is severely limited by a near-absence of experimental work. We depend, therefore, mainly on a comparison of field observations in our suggestions as to the effects of the edaphic complex.

Analysis of field data is complicated by intercorrelation between soil variables and between soil and climatic factors (French, 1974; Heal & French, 1974). Simple correlations of soil nutrients with decay rates are generally very poor, but there are trends of increasing losses with increasing concentrations of major soil nutrients, particularly if data are from sites with similar climatic patterns and for the same litter quality. Edaphic effects are most obvious in warm oceanic climatic conditions, i.e. where limiting climatic effects are minimised.

Comparison of decomposition rates of both natural litters and cellulose with site characteristics (Fig. 19.18) and with specific soil variables shows a trend of increasing losses with increasing pH and nitrogen. A more diffuse trend is observable in relation to 'available' phosphorus and potassium, but there is no apparent relation between litter decomposition rates and magnesium concentrations. The C:N ratio shows a threshold effect at about 23–25, high decay rates being confined to soils in which organic matter has a ratio at or below this level.

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There is a positive relation between decomposition rate and calcium concentration but there appear to be two separate trends, at differing intensities, depending on whether the soil is a peat or a mineral soil. There are also indications of interactive effects of phosphorus and calcium, again with two trends influenced by the organic matter content of the soil. The response of decay rate to increasing phosphorus or calcium is more pronounced when the organic content of the soils is above about 80 %. The extent to which the effects of calcium are causal nutrient effects, rather than via pH, is not clear. The combined effect of phosphorus, calcium and organic matter concentrations is probably responsible for much of the approximately three-fold variation in litter decay rates which occurs within any given climatic regime.

In the peat site at Glenamoy, the grassland has been fertilised and decomposition of cellulose is much more rapid on the grassland than on the unfertilised bog. Addition of nutrients to cellulose placed in the bog produced no significant change in the rate of decomposition in the surface layers but, at 4–8 cm, phosphate (0.4 %) caused a three-fold increase in decomposition rate, ammonium nitrate a doubling and calcium carbonate and combined nutrients a small, but significant, increase. At 16 cm, phosphorus, calcium and combined nutrients caused a significant decrease in decomposition (Rosswall, 1974). Similar experiments at Stordalen showed a significant increase in decomposition of cellulose with added nitrogen (protein, urea, ammonium, nitrate), but not with phosphate (Berg *et al.*, 1975). At Moor House microbial respiration in the peat responded to the combined addition of nitrogen (sodium glutamate) and a readily available carbon source, rather than to nitrogen separately or to other nutrients (Martin & Holding, 1978). Thus, the only common feature in these experiments, all on peat soils, is the positive response of decomposition to added nitrogen, contrasting with the lack of a relationship between weight loss and total nitrogen content of litter (Van Cleve, 1974). Experiments in which large concentrations of nitrogen, phosphorus and potassium were added to taiga sites in Alaska showed that rates of respiration and microbial biomass were increased slightly in the litter layer, but were depressed to 25–50 % of the control values in the fermentation and humus horizons (Van Cleve, 1974). The possibility of toxicity of high concentrations of nutrients is indicated by these experiments, but the responses of microbial populations over short periods of time, even over years, may differ from long-term response through adaptation and selection of the population.

Summary and conclusions

The control of the rate of decomposition (D) may be summarised as $D = f$ (temperature, moisture, edaphic factors, substrate quality). In the Tundra

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Biome there is a broad latitudinal and altitudinal gradient of temperature which provides a ceiling for decomposition. Given approximately optimal conditions of other factors, typical initial annual loss rate would be of the order of 100 % for warm oceanic, 50 % for warm continental, 30 % for cold oceanic and 20 % for cold continental conditions. This represents a five-fold difference over the temperature range of the tundra sites, although local topography may modify the temperature regimes with a climatic site. The effects of various factors tend to be multiplicative rather than additive and may be interactive as shown by the decline in optimum moisture as temperature increases. Limitation resulting from poor substrate quality, e.g. in dwarf shrub and moss communities, can reduce these initial loss rates approximately five-fold, i.e. to 20, 10, 6 and 4 %, respectively. Given the further constraints of sub- or supra-optimal moisture and low soil pH or nutrients, losses may be reduced to the order of 6, 3, 2 and 1 %, respectively.

The definition of the mechanisms involved in the decomposition of litter is summarised in the decomposition model (Bunnell & Scoullar, this volume). Moisture is represented as acting directly on respiration and also as influencing oxygen availability through the blocking of channels and pores in the substrate. The effect of the chemical composition of the substrate is represented through the optimal respiration rate at 10 °C, and the effect of temperature conforms to defined Q_{10} relationships. Comparison of model outputs and independent observations for various sites shows that the seasonal patterns and annual losses in decomposition can be predicted with reasonable accuracy through the mechanisms defined in the model.

The depth profile

The observed range of loss rates represents initial losses which, in all cases, decline with time as the more readily decomposable compounds are re-moved. The rates are also modified in different parts of the soil profile which integrates with depth, a complex gradient of all the variables which influence decomposition. Soil temperature often changes very sharply with depth, from +20 °C or more in the litter layer to 0 °C at the interface of frozen and unfrozen ground. During most of the active season temperature is highest at the surface; however, at night and during the autumn freeze-up period, the gradient may be reversed. Unfrozen soil may remain at 0 °C, even after the surface soils have frozen. In non-permafrost areas near-surface soils are frozen during winter while deeper soils may remain unfrozen and support decomposition activity, albeit at a slow rate.

In most tundra sites a large part of the annual precipitation accumulates over the long winter as snow, and then is released suddenly as melt-water in spring. All sites have potentially high soil moisture at this time, even if the

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annual precipitation total is small. Thus, more than in other biomes, local drainage conditions determine soil moisture content in tundra. In low-lying habitats, especially where drainage is impeded by frozen ground, saturated surface soils result. Frozen ground may also prevent melt-water from reaching and recharging deeper layers in the soil.

Subsequent development of the soil moisture profile depends upon the balance between precipitation and evapotranspiration. In maritime sites cool, cloudy conditions limit evapotranspiration and summer precipitation may maintain moisture at greater than optimal levels throughout the soil profile. Under these conditions the water table may lie at or just below the soil surface, and anaerobic conditions easily develop. At the opposite extreme lie well-drained habitats in sites with a continental, summer-dry climate. Under these conditions evapotranspiration exceeds precipitation, leading to drying of the surface layers of the soil, while deeper layers usually retain sufficient moisture to support decomposition.

Finally, substrate quality also varies with depth. The majority of the above-ground vascular plant production plus moss and lichen production becomes available for decomposition at the ground surface. Most of the easily decomposed compounds are used quickly. By the time the material is covered by the following year's litter fall, there has been a relative increase in the concentration of the more slowly decomposing compounds. Thus, in as much as the depth profile represents an age sequence of material, quality declines with depth.

At the same time, at depths specific to the rooting strategies of the plant species involved, root production inserts new material each year into the soil profile. At least some tundra plants living in saturated soils transport oxygen through the roots to support growth and metabolism in the anaerobic zone. Thus, root production and subsequent death may occur at depths at which decomposition is largely suppressed by anaerobic conditions and root tissue may have a higher probability of accumulating as peat than above-ground plant parts.

The depth profile of decomposition activity is most clearly revealed by the cotton strip data (Heal *et al.*, 1974). Three general patterns emerged (Fig. 19.19):

(1) High losses at the surface; sharp decline at about 10 cm; low loss rate at depth. Characteristic of bogs without permafrost.
(2) Medium losses at the surface; gradual decline to about 10 cm, then loss rate remains constant. Characteristic of palsas.
(3) No marked changes down the profile. Characteristic of mineral soils and shallow peats.

The high surface rates at Moor House and Glenamoy reflect the climatic potential of these warm, moist sites. The steep decline with depth shows the
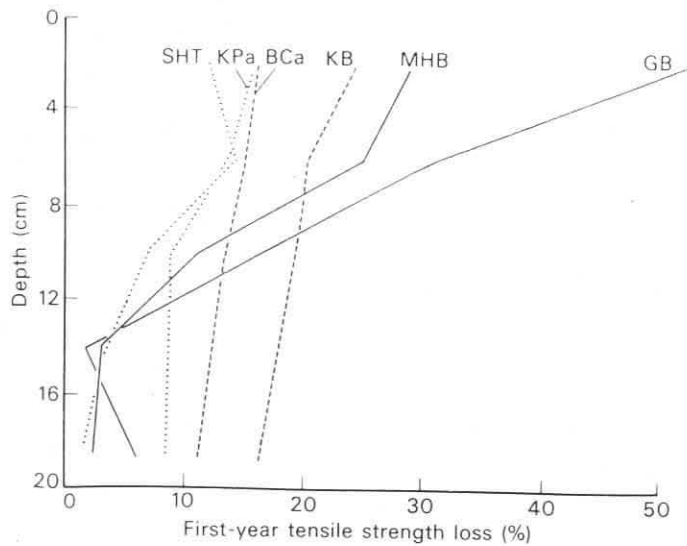
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Fig. 19.19. Profiles of decomposition of cotton strips in selected tundra sites. SHT – Stordalen hummock top. KPa – Kevo palsa, BCa – Barrow *Carex* site, KB – Kevo birch forest, MHB – Moor House bog. GB – Glenamoy bog, Profile types are 1, ─ ; 2, ····· ; 3, ──── (see p. 624). From Heal & French (1974).

effect of excess moisture and nutrient limitation, this decline corresponding to the position of the water table and anaerobic conditions. Even the high surface rates do not achieve the full climatic potential for decomposition. When better drainage and nutrient status occur, either naturally at the Moor House grassland or artificially at the Glenamoy grassland, much higher rates are recorded both at the surface and through the soil profile, illustrating the limitation of decay rate by local conditions of aeration and nutrient status.

Along a natural gradient of moisture and nutrient status across four habitats at Hardangervidda. surface rates showed much less variation. The depth profiles in the four habitats differ markedly (Fig. 19.20), the result, no doubt, of different combinations of factors. High surface rates and relatively little decline in rate with depth, and hence the greatest decomposition rate overall, occurred in the eutrophic dry meadow. The consistently lower rates in the wet meadow could result from a combination of supra-optimal moisture, and lower temperature and nutrient concentration than in the dry meadow. The snowbed, with the lowest surface rates and a steep decline below the surface, probably combines the limiting effects of short active season, low temperature and low nutrient status. The lichen heath habitat is particularly interesting. Surface temperatures may be high but the availability of water is much less than in the dry and wet meadows
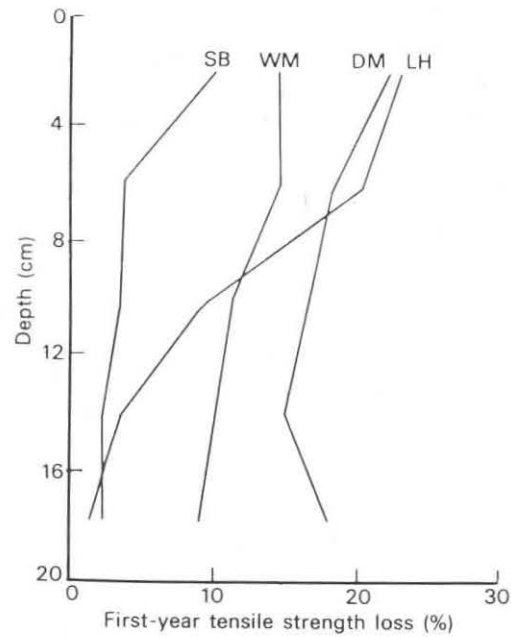
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Fig. 19.20. Profiles of decomposition of cotton strips at Hardangervidda. SB – snowbed, WM – wet meadow, DM – dry meadow, LH – lichen heath. From Heal & French (1974).

yet the lichen heath showed high rates of decomposition in the top two increments. The steep decline below this may result from excessive drainage in the sandy mineral soil underlying the organic layer.

Measurements of the weight loss of barley straw and of the annual loss of carbon in respiration indicate that decomposition rates decrease in the order: dry meadow > wet meadow > snow bed > lichen heath (Rosswall *et al.*, 1975). This corresponds with the results from cotton strips, with the exception of the lichen heath. Here we see the problem of comparing and interpreting different measures of decomposition; the barley straw measures first-year losses at the surface; the cotton strips measure the potential of the decomposer organisms to decompose an introduced substrate at different levels in the profile; respiration measures the losses from naturally-occurring organic matter throughout the profile and is influenced by the amount and quality of substrate present.

The decline in decomposition rate with depth is the sort of non-linear response that may produce large differences in organic matter accumulation from small differences in decomposition rate, and thus may have great importance in the ecosystem. A reduction in decay rate at the surface allows a larger proportion of the annual input to reach the depth at which decay

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rate falls; hence a larger proportion of the input is exposed to a slower rate of decay. This multiplies the effect of differences in surface rates, i.e. it acts as a positive feedback mechanism. Jones & Gore (1978), in a simulation of decay rates and peat accumulation in the Moor House blanket bog, found that change in decay rate with depth was a very critical parameter influencing rate of peat accumulation.

The insertion of below-ground production at depths of reduced rate of decomposition may also have a large effect upon organic matter accumulation. Thus (1) accumulated organic matter should contain a disproportionate amount of root tissue, and (2) change in the below-ground production should have a larger effect upon organic matter accumulation than a comparable change in above-ground production.

Decomposition and accumulation

The ratio of annual input of organic matter (I) to accumulated organic matter (X) provides a useful integrative ecosystem parameter. The decomposition rate (k) may be expressed as the average fraction of X that is lost in one year. Accumulation can then be represented by the linear differential equation relating rates of input and loss (Jenny, Gessel & Bingham, 1949; Olson, 1963):

$$\frac{dX}{dt} = I - kX.$$

Thus k is an integrative parameter describing the average condition, and as such it is very difficult or impossible to measure directly. If k does not change, the system described by the above equation converges upon a steady state at which $I = kX$ and $dX/dt = 0$. The steady-state ecosystem is defined as one in which, on average, organic matter is neither accumulating nor diminishing in quantity; that is, X_{ss} is constant; it shows no systematic tendency to change, although, of course, there may be seasonal or annual variations. Under these conditions, the ratio of I to X_{ss} can be used to indicate k:

$$\frac{I}{X_{ss}} = k.$$

This approach is technically applicable only to the steady-state condition. In a successional system $I \neq kX$; k falls as organic matter accumulates, even though the decay rate may be changing. In a peat-depositing system k asymptotically approaches zero and is more an indicator of the age of the system than it is of system dynamics; however, such systems are conveniently distinguished by their large accumulations and low apparent values of k, despite the violation of the steady-state assumption.

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The pattern of production and accumulation in tundra sites is shown in Fig. 19.21 with values of k calculated on the assumption that the systems approximate to a steady state.

In the dry sites, e.g. fellfields and beach ridges, relatively little organic matter accumulates because although the decay rates are low as a result of low moisture and a high proportion of woody material, the primary production is also low. As moisture increases the decay rates increase because moisture conditions are near optimal and the vegetation is often a meadow type with a small proportion of resistant material, e.g. wood and moss. The input from primary production also increases with increasing moisture, but little organic matter accumulates because of the high decay rates. It is only under very wet conditions that large quantities of organic matter accumulate, i.e. more than 50 kg m^{-2}. Under these conditions although surface decay rates may be high, waterlogging retards decomposition in the profile. In addition there is a feedback effect in that because of the low rates of decomposition and reduced contact of the plant roots with the mineral soil, nutrient supplies to the plants are low. Under such conditions input to the decomposer cycle tends to be of low quality. Where nutrient conditions are maintained at a high level, e.g. by flushing, the peats are less than about 50 cm deep as at the wet meadows at Hardangervidda and Devon Island.

The turnover rate for tundra systems, expressed by k, varies between 0.1 and 0.01 for most polar and alpine sites but falls to about 0.001 for bogs.
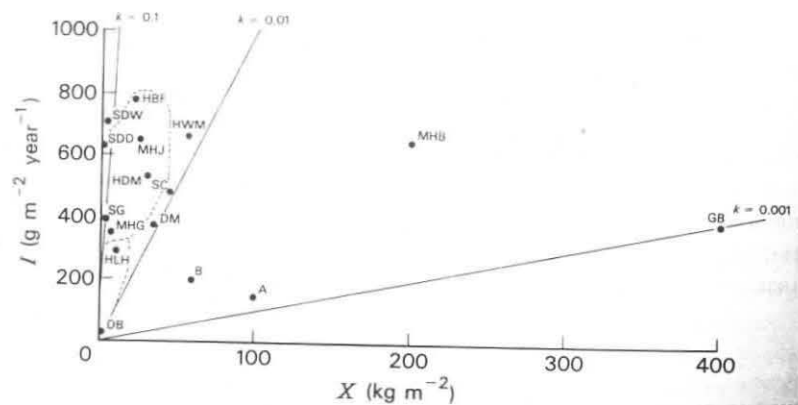

Fig. 19.21. Input (I) and accumulation (X) of organic matter in tundra sites. Inputs are total net primary production in g m^{-2} year^{-1}. Representative values of k derived from $k=I/X$ are shown. Site initials are HBP – Hardangervidda birch forest, HWM – Hardangervidda wet meadow, HDM – Hardangervidda dry meadow, HLH – Hardangervidda lichen heath, SDW – Signy Island *Drepanocladus* (wet), SDD – Signy *Drepanocladus* (dry), SC – Signy Island *Chorisodontium*, SG – Signy Island grassland, DM – Devon Island meadow, DB – Devon Island beach ridge, B – Point Barrow, A – Abisko Stordalen, MHJ – Moor House *Juncus*, MHG – Moor House grassland, MHB – Moor House bog, GB – Glenamoy bog.

Thus, it varies by two orders of magnitude. The turnover rate or fractional loss rate, when expressed as the number of years to reach 95 "‚ turnover ($3/k$) varies between 30 and 300 years for most sites and up to 3000 years for the bogs. The balance between input and loss from the decomposer cycle is represented by k, and when compared with temperate and tropical ecosystems (Fig. 19.22) there is apparently a shift in the balance that is broadly related to latitude. The change in balance indicates that the environmental conditions in tundra have a greater effect on decomposition processes than on primary production. Adaptation of the plants reduces the effect of low light regimes and both plants and decomposers show adaptation to low surface temperatures and nutrients. In contrast, decomposition is probably selectively inhibited by the lower temperatures within the soil, by sub- and supra-optimal soil moisture conditions and by low substrate quality.

The effect of change in amount accumulated is exacerbated in tundra where there is permafrost or anaerobic conditions. An increase in the amount of organic matter increases the insulation, the water-logging of the soil, and acid production from anaerobic decomposition, and further retards the decay rate. In addition, when the length of time taken to decompose is increased there is an increase in the proportion of material which becomes permanently locked up in the permafrost and in the anaerobic conditions of the bogs. This lock-up applies also to nutrients, thus reducing the nutrient recirculation to plants.

The reverse effect of an increase in decay rate and a decrease in accumulation can produce the dramatic thermocarst observed when organic soils are disturbed in permafrost areas.
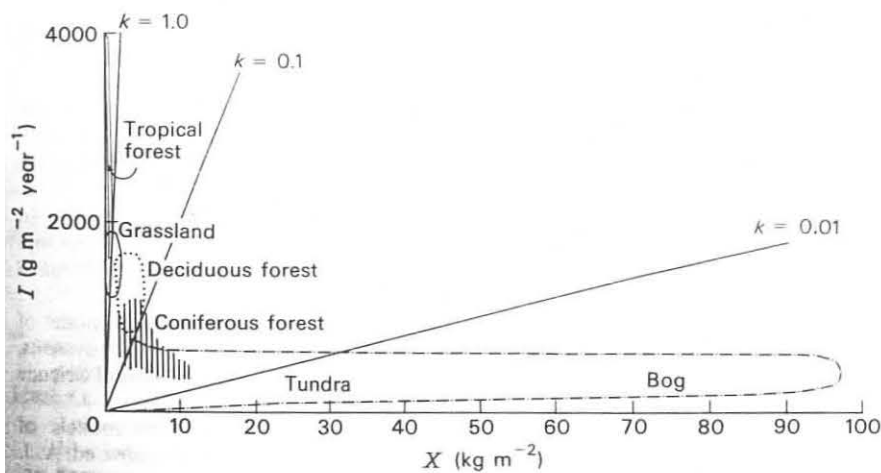
Fig. 19.22. Input (I) and accumulation (X) of organic matter in a number of biomes. Inputs are estimates of total annual net primary production. Data from Olson (1963), Rodin & Bazilevich (1967), and from Fig. 19.21.

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The decomposer cycle

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